VOL. 29, NO. 1 MAY 1960

THE JOURNAL OF ANIMAL ECOLOGY

ENTOMOLOGY LIBRARY
EU.431

EDITED FOR THE

BRITISH ECOLOGICAL SOCIETY

BY

H. C. GILSON

BLACKWELL SCIENTIFIC PUBLICATIONS · OXFORD

PUBLISHED TWICE A YEAR FORTY SHILLINGS NET

ANNUAL SUBSCRIPTION POST FREE SIXTY-THREE SHILLINGS

UNITED STATES OF AMERICA AND CANADA ELEVEN DOLLARS

NOTICE TO CONTRIBUTORS

Contributors are asked to study these notes with care in order to save themselves and the editor unnecessary work in the revision of manuscripts.

1. All correspondence should be addressed : **The Editor, Journal of Animal Ecology, The Ferry House, Ambleside, Westmorland.**

2. TEXT. MSS should be typed double-spaced on one side of the paper, leaving top and left-hand margins at least an inch wide. Latin names of genera and species, **but nothing else,** should be underlined. Dates should be in the form '1 January 1956, 25 June', etc., not 'Jan. 1st., or with the month indicated by a figure. Text-figures are to be referred to as 'Fig. 1', etc. In the use of symbols, signs and abbreviations *British Standard 1991 : Part I : 1954* should be followed, including the omission of all unnecessary full stops.

The *Journal*'s conventions regarding cross-headings should be followed, but they should not to be used too freely, **nor should headings be underlined.** Only long papers need include a table of contents. The Royal Society's *General notes on the preparation of scientific papers* should be followed on points not mentioned here.

3. LATIN NAMES. Excepting those of British vertebrates, all Latin specific names should be followed by the authority when the name is first mentioned in the text or tables. Names must be verified either from a standard list such as Kloet and Hincks's *Check-List of British Insects* or by submitting the final MS to the experts who have supplied the identifications.

4. REFERENCES should be listed in alphabetical order at the end of the paper in the form:

Vevers, H. G. & Fisher, J. (1938). The 1938 census of gannets (*Sula bassana*) on Ailsa Craig. *J. Anim. Ecol.* **7,** 303-4.

Titles of journals should be abbreviated according to the *World List of Scientific Periodicals*, except that the English usage of capitals for adjectives should be followed. Any reference not personally seen should be marked with an asterisk. **Nothing** except Latin names of genera and species should be underlined, nor should titles of papers or books be put in inverted commas.

5. TABLES should be set out on separate sheets and numbered in arabic numerals. So far as possible sufficient description should be included in the headings to make tables self-explanatory. The layout of tables should be kept as simple as possible; they are not printed 'boxed'.

6. TEXT-FIGURES. Drawings should be in jet-black indian ink, preferably on Bristol board. Shading must consist of lines or dots, not of half-tone washes. If the addition of mechanical stippling or hatching is required the area should be indicated by hatching lightly in blue pencil. Drawings should be arranged or grouped so that after suitable reduction a figure about 5 in. wide results. Graphs should be drawn on paper ruled in blue or faint grey; axes and graduation marks must be drawn in indian ink. All lettering, numerals and arrows should be shown lightly in pencil for insertion in uniform style by the blockmaker. The author's name and the number of the figure should be written on the back of each. Legends for figures should be collected together at the end of the MS.

7. PLATES. Photographs will only be used to illustrate important points which cannot conveniently be shown in any other way. Unmounted, glossy, half-plate prints showing good detail and moderate, but not excessive, contrast, are required. They should be numbered separately from text-figures, and each print should bear on its back the number and the author's name.

8. PROOFS. Page-proofs only will be sent. They should be returned with the least possible delay, and the minimum of essential correction should be made. Authors are requested to pay particular attention to the checking of numerical matter, mathematical formulae, tables and lists of names.

9. OFFPRINTS. Authors are supplied with 50 offprints gratis. Additional copies may be purchased if ordered when the proofs are returned. Contributors from abroad should order when sending their MSS. Offprints are sent out about a month after publication.

TIME AND SIZE AS FACTORS IN ECOLOGY

By ALAN BURGES

Hartley Botanical Laboratories, University of Liverpool

(BEING THE PRESIDENTIAL ADDRESS TO THE BRITISH ECOLOGICAL SOCIETY ON 3 JANUARY 1959)

It is inevitable that a great deal of ecology must be descriptive, yet it is surprising that when interest changed from the description of the structural aspects of vegetation to the examination of the changes which occur, the essential parameter of any changing system, time, has so seldom been mentioned. Succession has formed the subject of innumerable papers in the last forty years, yet in only a handful has the rate of the process been discussed. Even where the evidence was clearly available in the form of historical data or in the annual rings of the woody plants, the idea of time as an essential part of the process did not seem to occur to, or perhaps seemed unimportant to, the authors. In a random selection of over thirty papers on succession written between 1930 and 1940 none refers to the rate at which the process was taking place, and, although there were occasional papers in which the time element was discussed, these were very much the exception. In fact, as reference to the combined index of the *Journal of Ecology* shows, there is not a single entry for time, or for any other heading which suggests that the rate of the process was important. Yet these papers were written in a world in which speed was almost deified. So divorced has succession become from its legitimate spouse, time, that some ecologists have felt the necessity to invent a new term which leaves no opportunity for the time element to be overlooked; we no longer have a succession but a chronosequence!

The study of soils has in some respects been more fortunate than other aspects of ecology, although even here interest in time has been very restricted. Like plant ecology it passed through a descriptive phase and then became concerned with the developmental processes which lead to the formation of a mature soil more or less in equilibrium with its environment; nevertheless an emphasis was placed much earlier on the time factor. Dokachaev in his classical work on soils recognized the importance of the time element as early as 1881, but only occasionally did other workers give much attention to this aspect of soil development. Although almost every general account of soils describes the weathering of rocks, the formation of the soil and the subsequent development of a profile, the time scale of these changes is usually ignored. The papers dealing with the time aspect of soil development are so few that it would not be difficult to list them all. One of the earliest studies was by Dokachaev on the soil development on the ruins of the Staro Ladoga Fortress. The fortress was built in 1116 from slabs of Silurian limestone and granite boulders and when examined in 1880 after a period of 764

years there was a covering of 10-12 cm of soil. A similar investigation was made by Akimsev of the fourteenth-century fortress of Kamanetz in the Ukraine. The building material was of calcareous slabs and the soil development in this case varied from 10-90 cm in depth. One cannot assume that these soils were derived solely from the weathering of the rock, as wind-blown dust readily lodges on buildings, particularly once vegetation has become established, yet these observations do give a reasonable guide to the rate of weathering and soil development.

When we come to the problem of profile development more evidence is available. The information about the time scale is derived from several sources, from archaeology, historical records in the form of maps, geological evidence or from the age of the woody plants growing on the soil being studied. What is probably the earliest use of archaeological evidence is in the account by Ruprecht of the chernozem soils in Russia. He examined the mounds built by the Tartars in the steppes of European Russia 600 years ago. The material on these mounds had already developed into a chernozem 15-28 cm deep; on the surrounding land the soil was 60-150 cm deep. If the same rate of soil development had been maintained the main chernozems were thus between 2400 and 4000 years old. A summary of the Russian work will be found in Jenny (1941) and Joffe (1949).

The studies by Salisbury (1922, 1925) of the dune systems of Blakeney Point and of Southport represent some of the very few careful ecological studies in Britain in which the time scale has received any prominence. The Southport dunes have been formed on the northern side of the mouth of the River Mersey and he assessed their ages partly by the examination of old maps, *e.g.* Speed's map of 1616 and the Bold Estate map of 1736, and partly by counts of annual rings on the stems of *Salix repens*. In this way he obtained a time scale covering approximately 300 years and a series of samples along this time scale enabled him to follow the rate of soil development and plant succession. Of particular interest are his curves for the progressive leaching away of $CaCO_3$ and the corresponding fall in pH of the sand. He also gives a curve for a similar time series from Blakeney Point. Both curves show a fall in pH to a value of about 6·3-6·4 in a little over 200 years when most if not all the calcium carbonate had gone. Comparable curves for the accumulation of organic material are also given. These show that the organic content is still rising rapidly in the oldest dunes studied and that the system is still a long way from equilibrium.

The characteristic podsol profile has always attracted considerable interest perhaps because of the very pronounced horizon development, and it is not surprising, therefore, that several attempts have been made to determine the rate at which the horizons form. Tamm (1920) examined the soils left exposed after the drainage of Lake Ragunda in Sweden and showed that perceptible podsolization had occurred under a cover of pine-heath communities in about 100 years. The profile development was sufficient to allow the recognition of a thin bleached A_2 horizon and a dark B horizon. He considered that under the conditions in Sweden a well-matured podsol would be produced in 1000-1500 years and that beyond this period there was little further change. Work by Aaltonen in Finland

and Mattson in Sweden has been consolidated by Jenny (1941, Fig. 21) in a diagram showing the progressive formation of podsols in northern Europe plotted against a time scale. This diagram is of particular interest as it shows a gradual increase in depth of the A horizon but the zone of maximum accumulation in the B horizon becomes progressively nearer to the surface, a result at variance with results obtained in eastern Australia.

The Australian work (Burges & Drover 1953) was comparable with that of Salisbury and dealt with a large system of parallel sand ridges in eastern Australia and was based on a time scale derived from geological evidence. An aerial survey revealed an extensive system of parallel beach fronts between Woy Woy and Ocean Beach about 50 miles north of Sydney. Physiographic evidence suggested that beach building began with the end of the eustatic change in sea level which was estimated to have taken place about 4000 years ago. Beach formation is still proceeding so that a series of sand ridges were available on which the plant succession and soil development could be examined. As a first approximation it was assumed that the beach formation had progressed uniformly throughout the whole period. Subsequent studies of the soil profiles on the successive ridges supported the idea of a fairly uniform rate of beach formation and the absence of any marked discontinuities in the system suggested very strongly that there had been no major departures from a uniform rate of formation. Thus a transect running from the present beach front to the oldest ridges represented a time scale from 0-4000 years on which soil development and plant succession could be followed.

The initial stages of soil development were very similar to those recorded by Salisbury (1925). Calcium carbonate, originally present mainly as shell fragments, disappears in 200 to 300 years and the pH of the soil falls accordingly from the high initial value of 8·8 to 6·1 at a stage where calcium carbonate is no longer detectable. The accumulation of organic matter in the surface soil was also followed. This had reached an equilibrium value after about 100 years and remained fairly constant until after about 3000 years when a change in the dominant tree cover produced marked differences in the soil organic matter. Of most interest was the progressive development of the podsol profile. The vegetation was always dominated by members of the Myrtaceae. The very young dunes were rapidly colonized by a close shrubby growth of *Leptospermum laevigatum* which was replaced by small trees of *Eucalyptus botryoides* after 150-200 years. These in turn gave way to *Angophora intermedia* after 500-600 years. Over the first 2000 years the evidence suggests a fairly uniform rate of podsolization. The first clear evidence of iron movement was detected in profiles assumed to be about 280 years old. In these the upper layers were distinctly less yellow than the lower. The visual differences were confirmed by analysis. In soils assumed to be about 2000 years old a well-marked iron podsol was present. About half the iron originally present in the A_1 horizon had gone and most of this had moved to the B horizon. During this period of soil formation the soil-forming factors seemed to be acting uniformly and the major factor controlling soil development was time.

At a position in the series corresponding to an age of about 2500-2800 years there was an abrupt transition from sclerophyll forest dominated by *A. intermedia* to a forest very similar in appearance but dominated by *A. lanceolata*. This change was correlated with a change from iron to humus podsols.

Throughout most of the system investigated the main factor changing was the age of the soil. Two exceptions were noted. Along the road joining Ocean Beach and Woy Woy a few trees of *Pinus radiata* had been planted. The soil below the canopy of these trees was appreciably more podsolized than the surrounding soil, suggesting that the rates of the soil-forming processes were considerably faster under the pines than under the native *Angophora*. The other marked departure from the normal time effect on profile development was associated with the change from the iron to the humus podsol correlated with the change of the dominant plant from *A. intermedia* to *A. lanceolata*. Evidence that the change in soil type was associated with the change in plant species was obtained by examining isolated pockets of *A. lanceolata* which had become established early in the succession. These isolated pockets had the characteristic humus podsols.

The most detailed study of the time aspect of soil and vegetation development is that of Dickson & Crocker (1953). They examined an area in Mt. Shasta, California, where there had been a series of mud flows which had subsequently become covered by coniferous forests. The age of one of the mud flows was known from historical records and the others were determined from tree ring data. The oldest mud flow was clearly older than the life span of the trees and a conservative estimate of its age was made on the basis of morphological characteristics of the soil formed upon it; this soil was buried by a subsequent flow of known age. Five flows were studied, with ages of 27, 60, 205, 566 and 1200 years respectively.

Examination of the litter layer showed that many years were needed to reach anything approximating to equilibrium conditions. Initially the litter was almost entirely needles from *Pinus ponderosa*, the first colonist, but after 60 years twigs and bark formed over 20% of the litter. Pine cones and catkins did not form a significant part of the litter until the third sample, from the 205-year-old flow. The evidence suggests that about 500 years was required for the pine litter to reach an equilibrium, when the proportions of needles, twigs, bark, cones and catkins showed no further change. On the other hand, the material from the oak, *Quercus kellogii*, reached a stable condition much earlier. Associated with these changes in litter composition were corresponding changes in the organic content of the soil and of the forest floor. The total organic matter reached a maximum at 200 years and fell off slightly over the next 1000 years. The forest-floor organic material also reached a maximum at 200 years and then fell to about half this value by 566 years whereas the organic material in the soil continued to rise till the 566-year sample.

The total nitrogen in the system reached a maximum by 200 years and then remained surprisingly constant. Although the amount in the forest floor reached a maximum at the same time, it subsequently fell to about half of the maximum value, the nitrogen being transferred from the forest floor to the mineral soil system. Again it took 500 years to reach the equilibrium condition.

A similar study of the time factor in soil development was made by the same authors (Crocker & Dickson 1957) on the soils developing on the recessional moraines of the Herbert & Mendenhall glaciers in south-eastern Alaska. The ages of the different moraines had been determined by Lawrence and his colleagues (see Crocker & Dickson for references) by a series of 'painstaking shrub- and tree-ring analyses' integrated 'with much other data bearing on the surface age problem'. The time scale in this investigation extended over only 200 years, but this was sufficient to indicate that the nitrogen levels of the soil and forest floor had already reached an equilibrium by this time. The initial rate of nitrogen accumulation was high and this rate was maintained for about 60-70 years when it began to decline. The steady accumulation of nitrogen is correlated with alder dominance. The demonstration by Bond (1956) that the nodules of *Alnus* can fix atmospheric nitrogen lends interest to the correlation.

The general problems associated with considering time as an important factor in soil development have been reviewed in detail by Crocker (1952). Jenny (1941) had expressed soil development as a function of the various factors, climate, organisms, relief, parent material and time, in the following form:

$$s = f\,(cl,\ o,\ r,\ p,\ t)$$

However, this equation has been criticized by several writers on the ground that the factors cannot all be treated as independent variables. Criticism has been directed particularly at the assumption that time is an independent variable. Stephens (1947) suggested that the best way of treating soil development is to equate soil to the integral of the soil-forming factors against time as in the modified equation

$$s = \int (cl,\ o,\ r,\ p,\ w)\ dt.$$

where cl, o, r and p are as in Jenny's equation but w is water table.

Whatever the ultimate method adopted for formulating the process mathematically in practice the present approach to the practical problem has been to select areas for study in which most factors remain relatively constant and only one shows big changes. In the Woy Woy dune system for a period of about 2000 years, parent material, vegetation and relief did not appear to alter very much. We have little direct evidence regarding climate, but a study of the vegetation suggests that climatic fluctuations, if they occurred, were within the tolerance of the plant community and were therefore not greatly divergent from the present conditions. Time, therefore, was the dominant factor under examination. Departures from these conditions were fairly readily recognized once the general time sequence was established. Two examples of this are noteworthy. One due to the influence of change in tree dominant has already been mentioned, the other is due to change in relief. The general sequence of soil profiles described, referred to profiles taken from the crests of the sand ridges. If a different topographic area is considered, then a different sequence is obtained. For instance, in a ridge approximately 4000 years old the B horizon begins about 120 cm below the surface, whereas on the sloping side of the ridge the B horizon does not begin until 150 cm.

In ecological studies of forests the nature of the decomposition of the litter is of considerable interest. The rate of this decomposition can sometimes be determined by marking fallen leaves or branches and examining at suitable intervals, but often the rate of decay is too slow for this to be feasible. In following the decay of a mor type litter produced by *Casuarina* in Australia (Burges 1956) and *Pinus* in England (Kendrick 1959) marking of needles was used to follow the changes during the first year or two but for estimates of changes over longer periods alternative methods were used. In Kendrick's work the annual fall of litter was obtained by using suitable catchment trays. The litter was then separated into the different layers and the amount of material in each layer was determined. Typical needles from each layer were chosen and their dry weights measured. The ratios of these weights to the weight of a freshly fallen needle were used as conversion factors. The application of these conversion factors enabled the equivalent amount of fresh litter to be determined. Comparison of these figures with the measured year's fresh litter production allowed the approximate average time spent by a needle in each layer to be determined. While no great accuracy is claimed for the method it does give an idea of the length of time involved in the various stages of decay. The results obtained indicate that a needle when it falls spends, on the average, about 6 months in the L layer, approximately 2 years in the F_1 layer and 7 years in the F_2. All structure is lost in the H layer proper so that no estimate can be given for this layer by this method.

When we turn to a consideration of the seral development of plant communities the time factor is seldom discussed. This is surprising and the absence of an interest in the time scale has often led to the obscuring or neglect of fundamental problems in the succession.

Reference has already been made to Salisbury's (1925) work on sand-dunes. The youngest dunes were estimated as being about 2 years old and were colonized by *Agropyrum junceiforme* and *Ammophila arenaria*. A ridge about 6 years old was densely covered with vigorous *Ammophila*. By 14 years the *Ammophila* had become less vigorous and *Festuca arenaria*, *Cirsium* spp., *Senecio*, *Euphorbia* and *Carlina* were conspicuous. A ridge 55 years old still bore abundant *Ammophila* but this was unhealthy in appearance, and plants such as *Rubus caesius* and *Ononis repens* were conspicuous members of the community. The oldest dunes examined had an estimated age of about 280 years and although the vegetation had been greatly disturbed, patches of *Calluna* were present, probably representing remnants of the original cover.

In the Woy Woy dunes the plant succession could be followed much further, although the initial stages were considerably interfered with by man. Immediately behind the dune colonizers was a dense thicket of *Leptospermum laevigatum* and *Banksia integrifolia* about 2-4 m high and 100 m wide corresponding to the period of 10-100 years in the succession. A comparison of the plants in the younger and older parts of this community suggested that only two or three generations of plants formed this stage of the succession. The next phase was open low woodland of *Eucalyptus botryoides* which lasts probably for about 200-300 years. Here again

only a small number of generations of dominants can be involved, probably at the most only about two to four. The woodland dominated by *Angophora intermedia* occupied about 2000 years in the succession and is clearly a relatively stable unit. Although it was not possible to determine the age of the trees, because growth rings in many Australian trees bear no relation to annual cycles, comparison of trees with others of known age indicated that the oldest trees were between 100 and 200 years old. If this is correct, then between ten and twenty generations may occur in this phase of the succession.

Associated with the sequence of soil development at Mt. Shasta is a corresponding sequence of plant communities which have also been described by Dickson & Crocker (1953). The observations of Beardsley & Cannon (1930) had shown that pines colonized the mud flow within 1 or 2 years of its formation. The youngest flows examined by Dickson & Crocker were 27 years old and had a sparse community dominated by *Pinus ponderosa* and *Purshia tridentata*, but with only about 30% vegetation cover. The vegetation of the 60-year-old flow was characterized by uniform dense stands of *Pinus ponderosa*. Although there was evidence of as many as 30% of the trees becoming established later than the original colonization most of these late arrivals were thin and dying. The third flow, 205 years old, was still dominated by the original crop of pines, but the community was much more open. Grass and shrubs were present and *Quercus kelloggi* and *Libocedrus decurrens* became more prominent. The 566-year forest was once again a closed forest. Some of the original trees were still present but the gaps had been filled, often by *Pseudotsuga taxifolia*, many of which were less than 350 years old. The evidence points clearly to an invasion by *Pseudotsuga* soon after 200 years from the date of the mud flow. The forest is described as 'having all the features of a mature first generation forest'. The oldest forests which were at least 1200 years old were affected by logging operations but did not seem to differ greatly in structure from the 566-year forests.

In tropical forests succession is clearly much quicker. The classic case of tropical succession is in the development of the vegetation cover on the island of Krakatau (see Richards, 1952). Prior to the eruption of 1883, it was covered with luxurious tropical forest but as the result of the eruption, the island was completely buried by pumice and ash to a depth of about 30 m. Three years later there was already a distinctive shore vegetation and an inland community. Fourteen years after the eruption the centre of the island was covered by tall grass several metres high. Twenty-three years after the eruption the centre was covered by open grass savanna formed from trees characteristic of secondary forest. This savanna was still in existence nearly 36 years after the eruption, but 9 years later the trees had increased in size and number and nearly the whole of the savanna had been converted into mixed *Macaranga-Ficus* wood. The mixed woodland was very similar to the secondary forest common in the Malayan region after the primary rainforest had been cleared. Thus 45 years had been sufficient to produce a fairly typical secondary forest. How long it would take for this to be converted to forest of the primary type is not known.

A detailed account of the early stages in secondary succession in Nigeria is given

by Richards (1952) based on work carried out by Ross. The Shasha forest reserve was originally a belt of continuous rainforest but due to shifting cultivation by the natives it has become a mosaic of secondary forest of different ages surrounding the permanent settlements. Areas were selected which had been left uncultivated for $5\frac{1}{2}$, $14\frac{1}{2}$ and $17\frac{1}{2}$ years respectively. When the land is abandoned it is left practically clear except for a few standing trees and perennial crop plants but colonization is very rapid. One area which was clear in March had become covered by a dense growth of *Trema* seedlings a metre high in May. Three years after the clearings had been abandoned trees of *Musanga* were dominant. After 5 years there was already a well-defined second storey to the developing forest. After 15-20 years the *Musanga* trees die, thus this stage in the succession is occupied by a single generation. Other trees reaching 20-25 m take over the dominance, some of them being typical representatives of the high forest. The succession was not studied beyond the first 20 years but by this time it was clear that the new community was already approaching the climax forest, nevertheless a long period of time was still required before this stage was reached.

In many small units of vegetation the time scale can be obtained either by direct observations or by internal evidence based on growth ring data. The erosion complexes of the Cairngorms (Burges 1951) are examples of such units. At an altitude of 3000-3250 ft on the slopes of Cairngorm small communities of *Empetrum*, *Vaccinium* and the moss *Rhacomitrium* form complex units which are steadily eroded by the wind on one side but have a compensating forward growth on the lee side. Growth ring counts showed that the rate of movement was of the order of 1 m in 50 years. In a study of lichen succession on tree branches undertaken by Mr P. James at Liverpool, the time scale was determined partly by growth ring counts but primarily by counting the number of groups of terminal bud scale scars.

General considerations on time scales

Although the amount of evidence so far available concerning the time scale of ecological processes is very small, nevertheless it is already sufficient to indicate its importance. This is particularly true when problems of soil development and succession are being considered.

During the early stages of pedology, great emphasis was laid on climate as a controlling factor and there was a close parallel between the pedologist with his zonal soils in equilibrium with the climate and the plant ecologist with his climatic climax. With advancing knowledge it became increasingly apparent that other factors such as parent material and plant cover were often equally important in determining the course of soil development. Sometimes the actual direction of the process was controlled, at other times it was the rate of the process which was primarily affected. Unless a time scale can be put on the process it is often difficult to determine whether an equilibrium has been reached. Frequently a comparison of the time scales of different soil developmental processes will allow the evaluation of the importance of different factors involved in this process. In

the Woy Woy sequence it enables the effect of *Pinus radiata* in increasing the rate of podsolization to be determined, and the change in direction of the soil-forming processes from an iron to a humus podsolization associated with the change in the dominant tree to be recognized.

On the plant-succession side of the problem a consideration of the time scales emphasizes a number of aspects which have frequently been overlooked. First, it is clear that some successions require a very long time to reach the climax conditions even where there is no evidence of any deflecting or retarding influences. On the Mt. Shasta mudflows 500 years are required to produce a forest which might fairly be termed a climax. On the Woy Woy dunes 2000 to 3000 years may well be involved. A podsol may require 1200-1500 years to reach maturity in Sweden under conifers yet need 4000 years in Australia under trees belonging to the Myrtaceae. Even under tropical conditions, where growth rates are high and individual life spans often short, although a dense forest cover can be formed in 45-50 years the community still differs considerably from the climax type of forest.

Within the succession itself one of the most important aspects brought into prominence by attention to the time scale is the number of generations involved in each stage of the succession. In its simplest form a succession may be composed of single generations of each of the dominant species in each stage of the succession. On the other hand, each stage in the succession may be sufficiently prolonged to allow the development of a Watt (1947) 'Process and Pattern' phenomenon.

In the Woy Woy succession the initial stages probably consist of only one or two generations but the penultimate stage probably of ten to twenty. In contrast to this the Mt. Shasta sequence is essentially dominated by a single generation of long lived individuals of *P. ponderosa*. It is difficult to picture the situation involved in the development of a plant community such as the *Sequoia* or *Taxodium* forests of western America. If such communities developed via a succession, the seedlings of the first members of the presumed climax must have begun growth at least 4000 years ago. Such figures force us to put some successional patterns into a chronology more familiar to a pollen analyst than to an ecologist concerned with present-day vegetation. In general discussions of succession, it often appears as if the participants have begun by assuming that the time scale of the succession is short in relation to the rate of climatic change, and that the climate may be considered as uniform throughout the whole process. This is far from the truth and any discussion of a succession which has a time scale of hundreds of years must take into account the changing patterns of climate.

Even in smaller units the time scale must be related to the major climatic time scale. The erosion units on the upper slopes of Cairngorm may move at about a metre in 50 years but even in the 200 years which would allow a movement of some 4 m, important changes may have occurred in the local climate. A few weeks' difference in the length of the snow-cover may well determine whether the community is exposed to the full force of the late winter gales or not, and this in turn determines whether the community can maintain a closed cover or be torn to an erosion complex.

Within a stable community the development of the repetitive cycle of growth and breakdown can vary greatly in length. In Watt's Grassland A on the Breckland the full cycle may be complete in 4 to 5 years; thus many full cycles can occur in the duration of the community. In a complex forest of a long-lived species changing climatic conditions may lead to the disappearance of the community before many cycles have taken place.

In choosing my examples primarily from studies of successions, I do not wish to suggest that successions are the only way in which complex plant communities have developed. Very often one mature plant community may have invaded and replaced another mature community under the influence of climatic change such as had been suggested by Crocker & Wood (1947). It may well be that once a mature soil has developed the displacement of one climax community by another may be a faster process than the successional development of either. The evidence now accumulating from quaternary studies certainly indicates that at times there must have been very rapid replacements of one characteristic vegetation by another. Here again our best hope of elucidating the problem may be a detailed examination of the time scales involved.

The previous examples were chosen to illustrate continuous processes and to stress the need for placing a time scale on the changes which take place. There is a complementary aspect of the subject and that is 'at what time shall the observation be made?' Few of us live in the field and undertake continuous observations, and consequently most ecological results are based on records taken at relatively few points on the time scale. We are aware of the seasonal aspects of vegetation but few are conscious of seasonal drifts in plant communities or in their displacement over a short period of years.

The work of Lawson (1957) on intertidal zonation on the coasts of Ghana is a very beautiful example of the seasonal movement of the communities as a whole. Many of the species of seaweeds in the intertidal communities are relatively short lived so that there is a considerable turnover in the individuals forming the community every year. Careful observations revealed that the algal zones showed a seasonal periodicity in their position on the shore and that this movement could be correlated with the change in low tide levels occurring in daylight hours, over the 3 years. Not only did the tide curve offer some explanation for the seasonal shift of the zonation but also for the variation from one year to another.

Lawson was concerned mainly with species with a short generation time. In perennial species we must often relate the distributions not to the present conditions but to those prevailing at the time of establishment. Where the individuals comprising the community are thousands of years old such a view is readily accepted. Similarly the importance of a knowledge of the previous land utilization of an area can easily be appreciated. But often we are concerned with effects on a very much shorter time scale. A severe storm destroying part of the vegetation just at the time when propagules of a different species are available to recolonize the bare area could well alter the plant community over a wide area. Such events may often determine the pattern of the vegetation for many years. Exigencies of

University timetables and other weighty matters may restrict our field work but from time to time we should examine our time scale and see how much or how little of it is really familiar to us.

In the foregoing examples of succession and cyclic patterns, I have endeavoured to select those in which we have some knowledge of the time scales involved and in which this information has been derived from different kinds of evidence. Often the acquisition of such data involves very little additional work on the part of the investigator. That there are so many accounts of succession which have no mention of the time factor can only be explained on the grounds that the investigators did not consider time an important aspect of the process. May I make a plea that no investigation of a dynamic process in ecology be considered satisfactory unless due attention is paid to the rate at which the changes are taking place.

I would like now to turn briefly to my second point, the importance of size. As an undergraduate no piece of scientific writing impressed me more than Haldane's essay 'On being the right size'. Haldane with his interest in animals wrote of mice, rats and elephants and of angels and giant-killers, yet many of the principles which he so ably demonstrated are of wide application still. Despite this they are often overlooked. So often we are prepared to examine a technique with the greatest care, to test its validity with various statistical devices and apply it justly to the problem for which it was developed, then with almost glorious abandon apply the same technique to a different problem to which it may or may not be appropriate without any adequate check of its validity.

We frequently fall into such errors when we make a big change in the size of the units with which we are working. Nowhere is this more evident that in my own particular field, the ecology of the micro-organisms in the soil.

So many of our sampling methods and our techniques have been developed to examine communities such as forest or grassland that we are conditioned to a world in which our sampling unit, often the quadrat, is small in comparison with the extent of the community being sampled. Within this world we have been prepared to investigate the size and shape of quadrat most appropriate to give us the desired accuracy and to reveal or obscure any departure from random distribution of individual plants making up the community. The problem of sampling communities which may extend for only a few centimetres or perhaps even only a few millimetres, has received little attention. In the microbiology of agricultural soils it has been the usual practice to take a large number of samples often of 10-100 g and make some composite sample after thorough mixing, the whole emphasis being on the achieving of a statistically reproducible count of the organisms present. Provided sufficient replicates are used, statistical satisfaction can be attained. The biological interpretation of these results, however, is an entirely different matter.

Many of the processes taking place in the soil are of the nature of micro-successions or perhaps of the cyclic nature described by Watt. If we consider the litter which develops under pine forest the stages involved in the successive decomposition of the needles, while they may be very extensive laterally, often occupy only

a few millimetres in depth. Any technique which averages the conditions throughout such a series of communities will often obscure a great deal of the complexity and pattern of the system. A carefully randomized series of litter samples, in which the litter is sampled as a whole, provides only a fraction of the information desired and which could have been obtained with very little additional work. It is comparable to taking very large samples at random over the whole of a sand-dune system, with a method which ultimately gives a statistically reproducible list of the species and their abundance which occur in the area, without any reference to the successional communities. It may give a very satisfactory list of species which one may expect to find in such a geographical area but little more. If there is to be an advance in the ecological aspects of soil microbiology comparable with the advance made in higher plant ecology then one of the first steps must be a recognition of the size of the communities being studied. Often this will mean the recognition of units as small as a single pine needle or a seed coat.

An interesting example of the difficulties which arise when the size of the community or the organism is overlooked arose in the controversy which surrounds the natural occurrence of antibiotics. With the discovery and wide use of penicillin a search began for other antibiotics. Numbers were soon found and it was quickly assumed by many people that the ability of an organism to produce an antibiotic was an advantage to the organism in the fiercely competitive world in the soil. However, initial attempts to demonstrate the presence of the antibiotics in soil were unsuccessful. Soil was inoculated with the antibiotic-producing organism and after a time attempts made to extract the antibiotic without success. These and other experiments led many workers to conclude that antibiotics were artefacts of the laboratory and played no part in the natural life of the organisms. When the problem was examined more critically and due regard paid to the nature and the extent of the substrate occupied by the fungus or the actinomycete, a different result was obtained. If small pieces of organic material, *e.g.* pieces of straw, are added to the soil, these can become invaded by an antibiotic-producing species and a local concentration of the antibiotic be produced, sufficient to allow isolation and characterization. Similarly when seed is sown the seed coats are capable of acting as the habitat for the antibiotic producers and local accumulations of the antibiotic occur of sufficient concentration to produce an inhibiting effect on other organisms (Brian 1957). Sampling the soil as a whole would almost certainly fail to reveal the presence of any detectable quantities of antibiotic.

Because of the spectacular nature of their action the natural occurrence of antibiotic production has excited a great deal of interest. From the evidence at present available it seems that similar problems exist in terms of micro-distribution of mineral nutrients and in hydrogen ion concentrations. When individual needles of *Casuarina* were taken from different layers of the decomposing litter and their pH determined there was a range of just over two pH units. Since it is the individual needle which forms the micro-habitat, clearly an average pH value is of limited value in attempting to understand the community.

Nowhere is the size problem less appreciated than in general discussions of the

soil population. A grain of soil from an agriculture field contains perhaps 200 000 000 bacteria, let alone sufficient spores and hyphae to give a count equivalent to 500 000 fungi and 600 000 actinomycetes. This clearly conveys the picture of a densely populated habitat yet in terms of space occupied by individuals it is far from the truth. Direct observations by any of the usual ways, or by embedding and sectioning the soil, show that it is difficult to find many bacteria or fungi. Most of the habitat appears completely uncolonized. A simple consideration of size shows that this is not surprising. A spherical bacterium 1 μ in diameter has a volume approximately 0·5 μ^3. 2×10^8 of these will occupy a volume of $1{\cdot}0 \times 10^{-4} cm^3$ thus less than $\frac{1}{10000}$th of the soil would be occupied by the bacteria. On the other hand, the distance to which products of these micro-organisms can diffuse is very great indeed when measured in terms of the size of the organism itself.

While the difficulties associated with size are most readily appreciated when examples are taken from the ecology of micro-organisms, many of the same difficulties are also there in the investigation of some higher plant communities. In the study of rupicolous communities for example a failure to appreciate the size factor has been primarily responsible for the unsatisfactory way in which these communities have so far been treated. A rock face can usually be divided into a series of microhabitats each with its particular microclimatic conditions, topography, etc., and corresponding to these are micro-associations which are more homogeneous and 'objective' than the heterogeneous pseudo-association occupying the cliff as a whole. For example, certain types of rupicolous microhabitats have been described for the Mediterranean countries and these habitats appear to be generally valid for the region as a whole. Study of many pieces of vegetation described as associations shows that they are not really distinct associations but can be divided up into micro-associations correlated with microhabitat and corresponding with micro-associations known from other places (Heywood 1953). The problem is essentially one of scale, and the size of the units used in the examination of the communities.

In trying to illustrate my points, I may perhaps have confused you with too many apparently unconnected examples, but if by chance I have succeeded in making you look at your watch or your ruler with new interest, I shall have achieved something.

REFERENCES

Beardsley, G. F. & Cannon, W. A. (1930). Note on the effects of a mudflow at Mount Shasta on the vegetation. *Ecology,* **11,** 326.

Bond, G. (1956). Evidence for fixation of nitrogen by root nodules of Alder (*Alnus*) under field conditions. *New Phytol.* **55,** 147.

Brian, P. W. (1957). The ecological significance of antibiotic production. *Symposium of Soc. gen. Microbiol.* **7,** 168.

Burges, A. (1951). The ecology of the Cairngorms. III. The Empetrum-Vaccinium zone. *J. Ecol.* **39,** 271.

Burges, A. (1956). The release of cations during the decomposition of forest litter. 6 *ième Congr. de la Sci. du Sol.* **II,** 741.

Burges, A. & Drover, D. P. (1953). The rate of podsol development in the sands of the Woy Woy district, N.S.W. *Austr. J. Bot.* **1,** 83.

Crocker, R. L. (1952). Soil genesis and pedogenic factors. *Quart. Rev. Biol.* **27,** 139.

Crocker, R. L. & Dickson, B. A. (**1957**). Soil development on the successional moraines of the Herbert and Mendenhall glaciers, south-eastern Alaska. *J. Ecol.* **45,** 169.

Crocker, R. L. & Wood, J. G. (**1947**). Some historical influences on the development of South Australian vegetation communities and their bearing on concepts and classification in ecology. *Trans. Roy. Soc. S. Austr.* **71,** 91.

Dickson, B. A. & Crocker, R. L. (1953). A chronosequence of soils and vegetation near Mt. Shasta, California. I and II. *J. Soil Sci.* **4,** 123 and 142.

Heywood, V. H. (**1953**). El concepto de associacion en les comunidades rupicolas. *Anal. Inst. Bot. A. J. Cavanilles, Madrid,* **11,** 463.

Jenny, H. (**1941**). *Factors of Soil Formation.* New York.

Joffe, J. S. (**1949**). *Pedology.* New Brunswick.

Kendrick, W. B. (**1959**). The time factor in the decomposition of coniferous leaf litter. *Canad. J. Bot.* **37,** 907.

Lawson, G. W. (**1957**). Seasonal variation of intertidal zonation on the coast of Ghana in relation to tidal factors. *J. Ecol.* **45,** 831.

Richards, P. W. (**1952**). *The Tropical Rain Forest.* Cambridge.

Salisbury, E. J. (**1922**). The soils of Blakeney Point. A study of soil reaction and succession in relation to plant covering. *Ann. Bot. Lond.* **36,** 391.

Salisbury, E. J. (**1925**). Note on the edaphic succession in some dune soils with special reference to the time factor. *J. Ecol.* **13,** 322.

Stephens, C. G. (**1947**). Functional synthesis in pedogenesis. *Trans. Roy. Soc. S. Austr.* **71,** 168.

Tamm, O. (**1920**). Bodenstudien in der nord-schwedischen Nadelwaldregion. *Medd. Skogförsöksanst. Stockh.* **17,** 49.

Watt, A. S. (**1947**). Pattern and process in the plant community. *J. Ecol.* **35,** 1.

THE BIONOMICS AND ECOLOGY OF THE RED TREE ANT, *OECOPHYLLA* SP., AND ITS RELATIONSHIP TO THE COCONUT BUG *PSEUDOTHERAPTUS WAYI* BROWN (COREIDAE)

By F. L. VANDERPLANK

Coconut Pest Research, Zanzibar

(With Plates 1 and 2 and 1 Figure in the Text)

Way (1951, 1953) and Vanderplank (1953) have pointed out the beneficial effects of the red tree ant, *Oecophylla* sp., in controlling *Pseudotheraptus wayi* Brown (Coreidae) which causes a considerable loss of nuts from the coconut palm, *Cocos nucifera*, in East Africa. Similar protection is given from a similar coreid pest, *Amblypelta cocophaga* China, by *Oecophylla smaragdina* Enery, found in the British Solomon Islands Protectorate (Lever 1935, Lever & Phillips 1936, Phillips 1940, Leach 1949, O'Connor 1949, 1950 and Brown 1954, 1955). It has not been possible to undertake a detailed investigation of *Oecophylla*, and this paper describes various aspects that have been observed while investigating the ecology of *Pseudotheraptus wayi*. Way (1954a) gives an account of the life history of *Oecophylla* in Zanzibar, and Way (1954b) an account of its association with the scale insect *Saissetia zanzibarensis* Williams. This paper supplements Way's published observations.

The African species of *Oecophylla* has been described by Latreille as *O. longinoda* but I doubt whether there are sufficient grounds for separating it as a distinct species from *O. smaragdina* F. except perhaps on its geographical distribution. This is given in detail by Way (1954a). In addition I have observed *Oecophylla* in many inland areas of tropical Africa, and up to 4000 ft altitude, where the eco-climate is suitable. I have particularly noted its presence in Mwanza on Lake Victoria, Tanganyika, and in riverine evergreen forest fringing seasonal streams and rivers in the Shinyanga district of Tanganyika 3800 ft above sea level. I have observed *Oecophylla* in riverine vegetation in various parts of Tanganyika, Northern Rhodesia, Belgian Congo, northern Nigeria and the British Cameroons.

LIFE HISTORY

(*a*) *Laboratory experiments in rearing colonies*

Winged females emerge from the leaf-nests in considerable numbers following heavy rain storms from November to May each year. Winged male and female forms occupy different nests, although dealated males have been observed in the same nest as alate females, and from any particular colony the winged males emerge some days or even weeks before the winged females. Although with most species of ants mating usually takes place during or immediately after the nuptial flight, I have not observed mating to take place with the maiden flight of *Oecophylla*.

A large number of alate females have been captured as they emerged from their original nests, and all those kept in the laboratory have reproduced all forms, which suggests that they had been inseminated. The liberated males will enter nests of other colonies, and although a proportion are seized and killed by the worker ants, some enter unmolested. It is thought that such males may enter into coitus with the females before liberation in such nests.

Captured alate and dealated females can be reared without difficulty in the laboratory by placing them in a cell made by threading a living leaf (attached to a potted plant) through a match-box, so that the bottom of the match-box is covered by the upper surface of the leaf. Small clove trees were the most convenient plants in Zanzibar for this work, and a small seedling from 12 to 18 in. high could support from ten to fifteen match-boxes. Four batches of twenty winged females on four clove seedlings in each batch were set up. One batch was placed in a controlled cool chamber at 24° C, the second batch kept at room temperature in the laboratory which averaged 28° C, the third and fourth batches were kept in incubators at 30° C and 33·3° C. All females shed their wings on the first or second day, and oviposited one ovum or more within 48 h after being placed in the match-box-leaf cells. Table 1 gives the time taken for the ova to hatch, duration of larval and pupal stages and total time from laying of the ova till the mature worker emerged.

Table 1. *Time taken for development of ova, larvae and pupae of* Oecophylla *sp.*

Temperature (° C)	Number of days taken for ovum to hatch	Duration of larval stage (days)	Duration of pupal stage (days)	Total days from ovum to adult
24	12½	25	12	50
28	6½	14	5	25
30	5½	9	3	18
33·3	4	All died		

The dealated females did not feed during this period, and produced an average of sixty-five eggs each. The larvae were fed by the 'queen', which presumably used her food reserves. All the colonies were sprinkled with rain water daily and the 'queens' were regularly observed drinking from a drop of water resting on the leaf. The match-boxes were left open, the gap being large enough for any workers to pass but insufficient for the 'queen' to escape. As soon as the larvae were large enough, about 6 days old in the 28° C batch, the 'queen' used these to spin silken webs across the entrance to the cell. Small perspex windows had been fitted to all the match-boxes used in this experiment (Pl. 1*A*).

It will be noted that at 33·3° C the larvae failed to develop. Another experiment was carried out later keeping the 'queens' at 16° C. At this temperature they laid numerous eggs and most of them lived over 4 months without food, but all the eggs failed to hatch. At an average temperature of 28° C 25 days must lapse before the first workers emerge. Even then 2 or 3 days pass before these workers, which are intermediate in size, cut a small hole through the silken web and search for food.

A

B

A. A 'queen' *Oecophylla* tending eggs in a colony 15 days old at 28° C.
B. *Oecophylla* making a leaf nest: *a*, a soldier with a larva sewing leaves together; *b*, a soldier pulling leaves together; *c*, a worker.

(*Photographs by the author*

(*Facing p. 16*)

At this stage the young colonies were transferred to separate potted clove seedlings kept on an ant-proof table. All these seedlings had a number of scale insects *Saissetia zanzibarensis* Williams. The young workers did not solicit these scales for honeydew, but seized some of them and took them to the nest, where they were devoured. It was not possible to tell whether the worker regurgitated this food and fed the 'queen' or whether they fed her with small pieces torn off the dead scale, but they did immediately start feeding her.

The batch of twenty young colonies reared at normal laboratory temperature were divided into two groups. One group was given small amounts of honey diluted with 75% distilled water, and the other batch were given *Drosophila* larvae and worker termites, which they took quite readily. When the colonies were 45 days old (time is taken from the day the 'queens' were captured), they had sixteen to twenty active workers each. From 80 to 100 days old the colonies moved out of the match-boxes and made their own leaf-nests. These are constructed by the large 'worker-soldier' ants pulling the leaves together, and using larvae from about 1 or 2 weeks after hatching as a source of 'silk' to sow the leaves together (Pl. 1*B*). This activity usually commences in the evening and is carried out during the night. Way (1954a) gives references to various workers who have described this nest-building or repairing damaged nests, and adds his own observations. When the above colonies were about 100 days old, there were obvious differences between the two batches. The ten colonies which were supplied with honey only, and which had by then devoured most of the scale-insects originally on the seedlings, were now producing small yellow workers, whereas the ten colonies supplied only with living insect food consisted of all large workers of a deep red colour. At this stage the colonies were transferred to a shelter in the garden, and placed on ant-proof tables. They were given two further potted clove seedlings, arranged so that the leaves all came in contact with each other. By the 200th day two of the colonies fed on honey and one fed on insects had died out, the remainder had increased in strength. Those fed on honey had about 100 active workers, the majority of which were small and all were of a yellow colour. These were not aggressive and generally retreated when the nest was handled. The nine colonies which had been fed on insects had about fifty large workers and only a few small workers. All were a deep red colour and extremely aggressive.

The batches were now subdivided, the surviving eight honey-fed colonies into two sub-batches of four colonies, 'A' and 'B' and the surviving nine insect-fed colonies into two sub-batches of four and five colonies 'C' and 'D'. Batch A was kept on its honey diet, batch B was offered insects, such as dipterous larvae, termites, various lepidopteran larvae and homopterans besides honey. Batch C was left on its insect diet, and batch D supplemented with honey. The ants in batch B did not take any interest in the insect food offered at first, and it was some weeks before they began to capture and feed on the insects regularly. Similarly the ants in batch D took no interest in the honey at first, and it was some weeks before they began to feed regularly on the honey. When the colonies were 300 days old, batch A had only increased very slightly in numbers and only small yellow workers

were present. Batch B had increased considerably in numbers and both small and large workers were present. The colours of these workers were now more red than yellow and they were more aggressive. Batch C had doubled their numbers, but were not so numerous as batch B, the majority of the workers were large, a deep red colour and they were extremely aggressive. Batch D had increased considerably in numbers, both small, intermediate and large workers were present. They were a deep red colour but not as dark as batch C; they were also aggressive, but not so aggressive as batch C. It was obvious by this time, that if the colonies were to progress they required more space, and they were transplanted on to young citrus trees growing in soil treated some months previously with dieldrin to render it ant-free. By the 400th day only two colonies remained in batch A, and these had only 100 or so small yellow workers. Three colonies in batch B remained and they now occupied several leaf nests. The fourth colony had disappeared and had probably migrated. Of batch C four colonies remained, but only had one or two nests and between 100 and 200 workers. Of batch D four colonies were now living under natural conditions and no further feeding took place. By the 500th day all the colonies in batch A had died out, the three colonies of batch B had increased in strength and were producing reproductive forms, and so were those of batch D. Two colonies of batch C were still existing. This experiment was repeated with similar results, and one colony fed solely on insect food has been kept for 4 years. It has about 1000 large workers, which are a deep red colour and very aggressive; so far it has failed to produce any reproductive forms.

(*b*) *Field observations*

Simultaneously with the laboratory experiments, a series of similar experiments was conducted in the field, using clove and citrus trees. A branch was protected against other species of ants by a band about 1 ft wide of 'Ostico D' and then a further 12 to 24 in. of the branch or the trunk of the tree were painted with 15% dieldrin in xylene below the sticky band. The alate females ('queens') were captured as they left the parental nest and placed in match-box-leaf cells, or on a leaf that had been rolled into a tube and pinned together. Fifty alate 'queens' were treated this way. Forty-six of these survived long enough to rear larvae and seal themselves in, and forty-two reached the stage when the first workers left the nest. Under these conditions most of the 'queens' laid four eggs a day during the first week. The first workers were seen from most nests between the 21st and 23rd days. This suggests from the data in Table 1 that the average temperature in the nest in the field is higher than the average outside (shade) temperature. This is not unexpected, since the sun shining on the match-box-leaf cell or rolled leaf during the day, and the insulative effect at night, would account for the inside temperature being higher. Of these colonies 70% flourished during the first 100 days, but declined later. The decline is considered to be due to the workers becoming trapped in the sticky bands; when these were wiped away or covered with paper, they were killed by the dieldrin bands. In some trees where

the dieldrin bands were covered with brown paper, most of the young *Oecophylla* colonies were attacked and wiped out by other species of ant. Only five colonies succeeded in establishing themselves, and one of these was wiped out by *Pheidole* sp. when a year old. Under natural conditions both large and small workers were produced, and, as usual with *Oecophylla*, the small workers tended and solicited homopterans for honeydew and the large workers preyed upon various insects, including a proportion of homopterans.

Observations have been kept on a number of artificially and naturally established colonies in the field. No males or females have been observed until the colony is at least 18 months old; more often the colony is 2 years old before reproductive forms appear. The males and females are usually found in separate leaf nests, although occasionally both have been found in the same nest. As already noted, the winged individuals emerge after heavy rain and are most frequently encountered between November and the end of May each year. No mating has been observed in flight or afterwards, but the majority of several hundreds of females which have been kept in the laboratory have all reproduced, and those which survived long enough have produced reproductive forms.

To see whether a colony that has been deprived of its 'queen' will produce another, some forty colonies in the field have been deprived of their 'queens' at different seasons. Only one dealated 'queen' has to date been found in any colony. All colonies deprived of their 'queen' diminished in numbers and eventually died out. Attempts were made to introduce dealated 'queens' from other colonies and alate 'queens' taken on their maiden flight; all were destroyed immediately.

Some of the techniques used by beekeepers were tried with 'queen-less' colonies of *Oecophylla*. A gravid alate 'queen' is enclosed in a small wire cage, which protects her from any attacks. One end of this cage is sealed with a plug of candy. When this is carried out with honeybees, by the time the workers have eaten their way through the candy and reached the queen, the scent of the queen has intermingled with that of the hive and she is generally accepted. In the tests carried out with *Oecophylla*, the workers took from 24 to 72 h to get through the candy, and on each occasion as soon as they reached the 'queen' they destroyed her. Another method is to anaesthetize the queen-less colony and the queen with carbon dioxide, placing the anaesthetized queen amongst the anaesthetized colony. By the time honeybees have recovered, they usually accept the introduced queen, but in the case of *Oecophylla*, although they made no attack for the first hour or so, they later attacked and destroyed her. A third method that I have used successfully on honeybees is to treat the whole colony with petrol vapour and then introduce the queen. The petrol vapour appears to destroy their sense of smell and by the time they recover it, the scents of the hive and introduced queen have mixed and the queen is accepted. This was tried on ten colonies of *Oecophylla* but failed each time.

With honeybees it is possible to combine a queen-less colony with one that has an inseminated queen. One method is to place the two colonies in close proximity, separated by a sheet of paper with numerous pin-holes pricked in it. The workers

of both colonies try to reach each other through the paper, but by the time they have managed to tear large enough holes, the scents of the two colonies have intermingled and they mix peaceably. This was tried with various *Oecophylla* colonies but failed on each occasion, one colony always succeeding in destroying the other. Another method which can be used with honeybees is to anaesthetize both colonies with carbon dioxide (or some other vapour) and mix the individuals of both colonies when anaesthetized. On recovery they usually mix without fighting. This was tried with several *Oecophylla* colonies, and although for the first hour or so after recovery they appear to have mixed successfully, later without exception the two colonies fought and one destroyed the other.

Colonies in the field vary in colour and the proportion of small to large workers (soldiers). Some colonies consist of very yellow individuals, and have a high proportion of small workers to large. These colonies are found to be tending numerous scale-insects, coccids or membracids or both, and not aggressive. On the other hand some colonies consist of very dark red large workers, and occasionally no small workers can be found. Such colonies do not appear to tend any homopterans, and are extremely aggressive. The majority of colonies are intermediate in all respects between these two extremes. Observations on the longevity of colonies have been in progress since 1952 and are not yet completed. Some 30% of the original 500 odd colonies observed are still flourishing after 5 years. The majority of those colonies which have vanished were destroyed by other species of ants, usually *Pheidole* sp.

Way (1954a) states that the 'queen' 'was always in a small nest from which worker ants carried batches of eggs along the pathways to other nests within the colony'. This does not agree with my own observations. Except when a colony had been disturbed or was moving from one nest to another, I have not observed workers carrying eggs but only half-grown larvae, which are used for spinning the silken webs. I have repeatedly observed the 'queen', usually at dusk or after dark, moving from one nest to another escorted by several hundred 'soldiers'. Undeveloped viable eggs have only been found in a nest where the 'queen' is present, and when such a nest is opened the 'queen' attempts to escape immediately, accompanied by a large number of soldier ants. From my own observations I conclude that the 'queen' moves from nest to nest to lay her eggs. Since these leaf nests only last a few weeks, a 'queen' has to move quite frequently to another.

POPULATIONS

To test the possibility of using radioactive compounds for tagging ants, an area in *uwanda* bush was selected which had numerous *Oecophylla* colonies nesting on low bushes 6 to 10 ft high. A colony which appeared to be surrounded by other colonies was selected and honey diluted with twice its volume of distilled water was offered in small tubes with wicks. Since this mixture was liable to ferment it was changed every other day. The *Oecophylla* at first did not appear interested, only a few workers taking the honey. After a fortnight the ants learnt that this was an easy supply of food, and some 10 ml were taken daily. Radioactive

phosphorus as a carrier-free orthophosphate in dilute hydrochloric acid (pH 3·5) and original activity of 8·83 mc/ml was used. One ml of ^{32}P solution was added to 5 ml of natural honey and 10 ml of distilled water. Radioactivity was detected by a portable radioactive ore detector (P.R.O.D.) made by E. K. Cole, Ltd. The background radiation in this area of coral and pockets of sand was 140 to 180 counts/min owing to the presence of radioactive sands containing small amounts of monozite (Ce La Di) PO_4 16% $Th_3(PO_4)_4$, and zircon. At some places on the ground the counts were as high as 200 to 300/min.

Some 30 ml containing 2 ml of radioactive orthophosphate were taken by the *Oecophylla* in the course of 48 h. The leaf-nests became strongly radioactive, giving counts of over 600/min. No significant counts over the background noise could be obtained from individual worker ants, but groups of more than ten workers gave a significant count above the ground radiation. The limits of the colony were clearly defined by the radioactive ants, and these did not intermingle with neighbouring colonies. The brood in the nests were also radioactive, and no doubt if larger quantities of ^{32}P were fed to the colony the virgin females could be rendered sufficiently radioactive for detection.

Several large colonies from clove or mango trees were collected and all individuals counted. The method used was to cut all the leaf-nests off as quickly as possible and drop them into large cloth bags. All the ants were killed by placing the bags in bins over cyanide. The largest colony collected had 192 leaf-nests, which contained 43 700 small workers, 18 994 large workers, 18 498 worker larvae and pupae, 657 larvae and pupae of reproductive females, no male larvae or pupae. Ova were not counted, and only one alate 'queen' was present. The total population was 81 849 individuals, larvae and pupae. It was considered that only 70% of the colony was collected, but the catch could be as low as 50%; the remaining workers either escaped from the nests or were out foraging. If this was so, the total population would be between 115 000 and 164 000. Way (1954a) states that the total population of a large colony was about 480 000 workers and 280 000 brood. The figures quoted by myself were from a larger colony than that analysed by Way and taken at the same period a year later.

Since the worker brood (large and small) takes about 20 days to develop and 37 492 worker brood were present, the 'queen' must have been producing eggs at an average of 930 per day. There were over 3·4 times as many adult workers as brood, and since many more escaped, the correct proportion may be nearer 6 or 7 times. If the population was relatively stable, the average longevity of the workers must be between 3·4 and 7×20, or 69 to 140 days.

PARASITES AND PREDATORS

The main predators of *Oecophylla* are other species of ant. The most important of these is *Pheidole megacephala* Mayr and *P. punctulata* Mayr. During dry periods, which are unfavourable to *Oecophylla* but favourable to *Pheidole*, the latter often attack *Oecophylla* colonies and will wipe out a complete colony within 2 or 3 weeks. The *Pheidole* invade *Oecophylla* territory in considerable numbers, a worker

will seize one of the *Oecophylla* soldier's or worker's legs, then another *Pheidole* will seize another leg until it is held down by ten or more *Pheidole*. The large headed *Pheidole* soldiers then appear and cut off the *Oecophylla's* legs, which are carried away by the *Pheidole* workers. The *Oecophylla* do not submit without trying to defend themselves, and during the fight they will destroy several *Pheidole* workers by cutting them in half with their mandibles. Plate 2.4 shows *Pheidole* attacking a living *Oecophylla* soldier on a leaf in the field. During wet periods the *Oecophylla* thrive and increase in numbers whereas *Pheidole* diminish, possibly owing to flooding of their nests, a thing which does not happen to *Oecophylla* in their leaf-nests. Under these circumstances *Oecophylla* often advance into *Pheidole* territory, and destroy any *Pheidole* which oppose them.

Two other indigenous species, *Crematogaster castanea* Sm. and *C. rectinota* Forel behave in the same way towards *Oecophylla* as *Pheidole*. Both species of *Crematogaster* nest in hollows and tunnels they excavate in dead branches or posts. Neither species is very common in Zanzibar, and they inhabit different ecological niches. *Crematogaster* occasionally establish themselves in the crowns of coconut palms, tunnelling in the debris which collects in the axils of the leaves. The ergates of *Crematogaster* are monomorphic and protect themselves in a similar manner to *Oecophylla*. They seize their prey or adversary with their mandibles and bend their abdomens over their thoraces, ejecting a milky fluid on the site where they are biting. The fluid ejected by *Crematogaster* is comparatively odourless to humans whereas that ejected by *Oecophylla* has a pungent acid smell. This fluid with both species acts as either a poison or an anaesthetic, and the victim becomes quiescent within a few minutes. *Crematogaster* does not appear to be predatory and does not usually carry off the dead *Oecophylla*. Both species of *Crematogaster* are polygynous. Another serious predator of *Oecophylla* sp. in Zanzibar is the imported 'crazy' ant *Anoplolepis longipes* (Jerdon). This species nests either in the ground or in the debris in the crown of the coconut palms. The ergates of *A. longipes* are monomorphic and eject a fluid from their abdomens in the same way as *Oecophylla*. They are intermediate in size between the large and small ergates of *Oecophylla*. *Anoplolepis longipes* is restricted to certain areas in Zanzibar, the largest approximately 5 miles south and east and 10 miles north of Zanzibar town. It advanced its boundaries between 1951 and 1954, but since then has retreated to its 1951 boundaries. When *A. longipes* advances it completely destroys any *Oecophylla* which appear to be terrified of this ant and usually try to escape. However, when it has cornered the *Oecophylla Anoplolepis* seizes it by its abdomen and ejects fluid over the site. This paralyses the *Oecophylla* within 1 or 2 min and the paralysed individual is carried off to the *Anoplolepis* nest. *A. longipes* are polygynous and colonies intermingle, so that it is not possible to discover where one colony starts or ends.

Another imported species of ant which preys on *Oecophylla* is *Anoplolepis custodiens* Smith. Mayer (1895) quoted by Steyn (1954) gives Zanzibar as a locality for *A. custodiens*. At that time Zanzibar included the coastal strip, but Mayer also gives other specific localities on the mainland. If *A. custodiens* did occur in

A

B

A. *Oecophylla* soldiers being attacked by *Pheidole* sp.: *a*, *Pheidole* workers cut in half by *Oecophylla* *b*, *Pheidole* soldiers engaged in cutting up the *Oecophylla*.
B. *Oecophylla* soldiers attacking a *Polyrhacis* worker.

(*Photographs by the author*)

(*Facing p. 22*)

Zanzibar Island at that time, it either disappeared or was present in such small numbers that it remained unnoticed until 1946 when it was found around a potted plant imported from the mainland. It has spread considerably since 1946 and now covers about 4000 acres around Zanzibar town, in territory previously occupied by *A. longipes*. *Oecophylla* is able to withstand the attacks of *Anoplolepis custodiens* better than those of *A. longipes*, but *A. custodiens* populations become so large that they eventually wipe out any *Oecophylla* within their territory. *Anoplolepis custodiens* do not eject any poison from their abdomens like *Oecophylla*, *Crematogaster* and *Anoplolepis longipes*, but they might possibly have a poisonous salivary secretion. Their bite is more painful than one would expect from a mechanical process, but it leaves practically no after-effect. Fights between *A. custodiens* and *Oecophylla* have not been observed. *Anoplolepis custodiens* are polygynous and the various colonies intermingle.

No other ant species have been found to destroy *Oecophylla* colonies, but most species of ants will destroy the lone 'queens' when they are starting a new colony. The following species have been observed to destroy lone 'queens' which were attempting to establish a colony, *Camponotus rufo-glaucus* Jerd, *C. vividus* Sm., *Camponotus* spp., *Tapinoma luteus* Em., *Cardiocondyla wroughtoni* For., *Triglyphothrix constanciae* Arnold, *Semonius schultzei* Forel, *Plagiolepis brunni* Mayr, *Myrmecaria striata* Stitz, *Macromischoides aculeata* Mayr and *Tapinoma melanocephalum* Fabr.

Way (1954a) notes that *Oecophylla* do not interfere with a species of spider which mimics the soldier ant. This spider has been identified as *Myrmarache* sp. (Salticidae). In old colonies it is often extremely common, and enters the leaf nests with impunity. I have observed it preying on *Oecophylla* worker larvae, although normally it does not appear to prey on *Oecophylla* but captures its own prey. Numerous small dipterans and hymenopterans are found in the nests of large and older colonies, and it is suspected that some of these are parasitic on the *Oecophylla* larvae.

A pseudo-scorpion (Cheliferidae) identified as *Hansenius* sp. becomes very common in older colonies. It hides in the crevices of the bark and in the leaf-nests of *Oecophylla* and preys on the *Oecophylla* ergates.

When a colony becomes heavily infested with the mimicking spiders, pseudo-scorpions and other suspected predators, the colony generally deserts its nesting site and moves completely within 48 hours to another tree or group of trees which may be from a few yards to as much as 400 yards away.

PREDATION BY *OECOPHYLLA*

Way (1954a) gives his observations on the predation by *Oecophylla* in Zanzibar. My observations do not differ in any way except he mentions that 'the "poison" does not seem to increase pain caused by the bite, nor does the pain persist after removal of the ant'. I cannot agree with this statement. I have allowed soldier ants to bite the back of my hand, and before they are able to squirt any fluid over the site of the bite, cut their abdomens off with a sharp pair of scissors. The bite

of the ant without any fluid is not painful, but the fluid makes the bite quite painful, and in my case I find the pain persists for 10-15 min after the ants have been removed. The local people also find the bite painful; hence *Oecophylla's* Kiswahili name *maji ya moto* or 'hot water ant'.

I have examined very numerous nests to ascertain *Oecophylla's* chief prey. Beside the various groups of insects mentioned by Way, I have found in some areas that workers and reproductive forms of termites comprise a large proportion of their prey. Most of the Zanzibar species of termites have been found in *Oecophylla* larders particularly the commonest in that area, *Macrotermes bellicosus* Smeath. Other worker termites taken from *Oecophylla* nests include *Microcerotermes zuluensis* Holm., *Amitermes unidentatus* Wasm. and *Trinervitermes segelli* Sjost. The next most frequent groups of insects found dead in the *Oecophylla* larders were various species of ants, such as *Polyrhacis schistacea* var. *rugulosa* Mayr (Pl. 2*B*) and var. *militaris* F., *Camponotus maculatus* Fab., *C. vividus* Sm., *C. rufo-glaucus* Jerd, *Paltothyneus tarsatus* Fabr. and *Dorylus nigricans* Ill., when the latter were in the area. Beside these ants, reproductive forms of most other species have been found from time to time, depending on their availability. Even reproductive forms of *Oecophylla* presumably from other colonies, and *Anoplolepis longipes* and *A. custodiens* have been found dead in the food larders. Honeybees particularly *Apis mellifera* L. var *adansonia* are very common throughout the year, and *Oecophylla* must take a heavy toll of this species. Other honeybees such as *Hypotrigoma* sp., *Trigoma* sp. and *Allodape* sp. are frequently found dead in the nests. *Oecophylla* will attack large insects such as *Oryctes monoceros* Oliver (Coleoptera) and *Platymerus rhadamanthus* Gerst (Reduviidae) but these species are strong enough to break away and escape. I have on several occasions collected both species some distance away from any *Oecophylla*, with one or two *Oecophylla* soldiers clinging to their legs.

The efficiency of *Oecophylla* as a predator is correlated with its numbers. A small colony with four to ten nests and 2000 to 5000 large and small workers will only occupy part of a coconut palm or medium-sized clove tree, although they may well forage over the whole of the palm and tree. The area immediately around the nests is kept clear of other insects, but the rest of the tree may be quite heavily infested with some pest. *Pseudotheraptus wayi* is able to survive on such palms and do considerable damage. Large colonies with ten to thirty nests and from 5000 to 20 000 workers are able to protect a palm from quite a considerable amount of *P. wayi* damage. Even with very strong colonies of 50 000-80 000 workers *P. wayi* generally is able to cause slight damage to the nuts.

Way (1954a) has already pointed out that *Oecophylla* do not interfere with certain lepidopterous larvae predatory on ant-attended Homoptera. Similarly they do not interfere with the larvae of the following Coccinellidae: *Cheilomenes sulphurea* (Oliv.), *Epilachna chrysomelia* (F.), *E. paykulli* Muls. and *Epilachna* sp. They destroy the larvae of the flatidid *Cryptoflata unipunctata* Oliv. which preys on *Pseudococcus citri* Risso. *Oecophylla* will prey on the first and second instar larvae of the citrus swallowtails *Papilio demodocus* Esp. and *P. nireus* L., but not

later instars. I have on several occasions observed third instars of *P. demodocus* and *P. nireus* being attacked by *Oecophylla*. The lepidopteran larvae erects its osmeterium and when this touches the attacking *Oecophylla* ergates, they retreat immediately and appear to be in considerable distress. These ants spend 10-30 min cleaning themselves and rubbing their heads against leaves. All observed have eventually recovered.

Way (1954a) gives a list of Homoptera solicited by *Oecophylla* and a detailed account of its relations with *Saissetia zanzibarensis* William. Beside soliciting these homopterans *Oecophylla* also preys upon them and most other species that occur in Zanzibar. *Oecophylla* have been observed soliciting and also preying upon the following membracids: *Oxyrhachis bisenti* Dist., *Oxyrhachis* sp. nov., *Eumonocentrus inclinatus* Cap., *Anchonobelus longicornis* Cap., *Centrotus bovinus* Dist., *Otinotus* sp. nov., a *Xiphopoeus* near *validicornis* Stal., and *Monocentrus* sp. nov. *Oecophylla* frequently tends *Empoasca* sp. (Cicadellidae).

MOVEMENTS

Way (1954a) records that the part of the tree selected for nest-building varied according to the season, and that the variation seemed to be correlated with the wind direction. He also notes that there is a tendency to construct nests on slopes facing the sun. I have noted that the change from one side of the tree to the other takes place before the change in the monsoon (wind). The sun is overhead early in October and again in the middle of March. The monsoons do not change direction until late in November and in April each year, yet *Oecophylla* move from one side of the tree to the other in late October and early November, and early in April each year, before the change in direction of the monsoon. This would indicate that the deciding factor is the position of the sun and not the prevailing wind, unless the ants move in anticipation of the change in wind direction. Nests are usually constructed in positions well exposed to the sun and not in the shade. As stated above, the complete colony will suddenly move to a new location if heavily infested with predators. Of 165 colonies observed for 3 years nesting in a block of 500 palms, eleven (6·6%) died out and seven (4%) moved to other palms. The application of some insecticides caused increased movement.

THE DISTRIBUTION OF *OECOPHYLLA* COLONIES IN COCONUT PLANTATIONS

Records have been kept from a total of over 16 200 palms searched either quarterly or half-yearly for *Oecophylla*, and in half of these individual palm yields have been kept from 18 months to 5½ years. Many of these plots have been used for experimental applications of various insecticides. The data obtained have been analysed to test whether *Oecophylla* is distributed at random, or whether the type of palm, its age and health have any effect. The analysis of these data is complicated by several factors particularly the distribution of *Pheidole* which are antagonistic to *Oecophylla*. In an area of 712 palms where both *Oecophylla* and *Pheidole* but no *Anoplolepis* species were present, and before any experimental

treatments were applied, the palms were numbered, their height (base to crown), the type of nut (based on a rather arbitary classification of size and colour) and the number of leaves the palm was carrying, were recorded. The palms were then searched and the dominant ant populations recorded. Table 2 gives the number

Table 2. *Distribution of* Oecophylla *in palms*

Height of palms (ft)	Number of palms	Number with *Oecophylla*	Percentage with *Oecophylla*
12–25	165	17	10·7
26–35	156	16	10·2
36–45	231	22	9·5
46–55	120	11	9·7
56–65	22	2	9·1
66–75	18	2	11·1
Total	712	70	9·8

of palms in the various height groups and those with *Oecophylla*. There is no significant difference between these groups, and so as far as the height of the palm is concerned, *Oecophylla* is distributed at random. Similarly Table 3 shows the palms classified according to the type of nut they bear. Again there is no significant difference in the numbers colonized by *Oecophylla* in each group, and

Table 3. Oecophylla *and nut types*

Type of nut	Number of palms	Number with *Oecophylla*	Percentage with *Oecophylla*
Large brownish-green	19	2	10·5
Large brown	8	0	–
Large green	51	5	10·0
Large yellow-green	27	3	9·9
Medium brown-green	132	12	9·5
Medium brown	44	3	6·8
Medium green	98	13	13·3
Medium yellow-green	89	10	11·2
Small brown	67	6	9·0
Small green	113	9	8·0
Small yellow-green	5	1	20·0
No nuts	59	6	10·2
Total	712	70	9·8

Oecophylla does not appear to show any preference for any particular type of nut. Table 4 divides the palms into three groups, those with more than forty leaves, those with less than twenty and those with between twenty and forty leaves. Again *Oecophylla* does not show any significant preference. The above data demonstrate that *Oecophylla* is distributed at random. When, however, an area of palms is marked to show which palms have *Oecophylla*, it will be seen (Fig. 1) that *Oecophylla* palms occur in groups. This would indicate a non-random distribution possibly due to the antagonistic behaviour of other species of ant. It would be interesting to see the distribution of *Oecophylla* in the absence of other species

of ant, but such circumstances do not appear to occur naturally. In some experimental areas where chemical insecticides have very considerably reduced all ant species, it has been possible to record the recolonization of the area by *Oecophylla* and other species. One such area that was dominated by *Anoplolepis longipes*, with 4% of the palms occupied by *Pheidole* sp., was treated by an air mist blower

Table 4. Oecophylla *and leafiness*

Number of leaves	Number of palms	Number with *Oecophylla*	Percentage with *Oecophylla*
>40	153	14	9·15
20–40	373	36	9·65
<20	186	20	10·75
Total	712	70	9·8

with a solution of D.D.T. and resin. Before the application of insecticide no *Oecophylla* were present in the area. During 2 years (1953 to 1955) of regular insecticidal treatment, *Oecophylla* increased while *Anoplolepis longipes* gradually decreased and had died out by September 1955. Nine months after insecticidal treatment had ceased, colonies of *Oecophylla* were found in 103 (37%) of 278

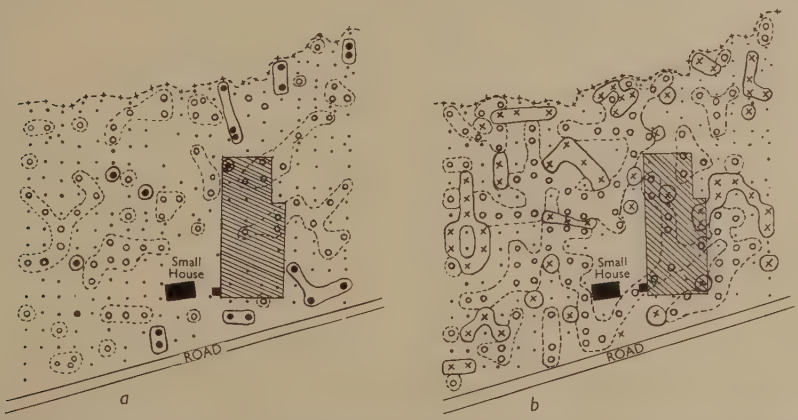


Fig. 1. Plan of plot B, Mazizini, *a* in March 1955, *b* in March 1956; the area shown is surrounded by continuous palm plantations. o, palms colonized by *Oecophylla* sp.; •, palms colonized by *Anoplolepis longipes*; ×, palms colonized by *Pheidole* sp.; •, palms not colonized by any of these three species; +–+–+, boundary of Government Plantation; the hatched area shows the coconut nursery.

palms and *Pheidole* sp. were nesting in the crowns of 65 (23%) palms (Fig. 1). The remaining 110 palms either were without ant colonies or had various species of small ants which would be destructive to unprotected *Oecophylla* and *Pheidole* 'queens'. Several statistical tests have been applied to these data, and these show that distribution does not depart from what would be expected to occur fortuitously.

THE VALUE OF *OECOPHYLLA* IN PROTECTING PALMS FROM *PSEUDOTHERAPTUS WAYI* DAMAGE

There is a considerable variation between individual colonies of *Oecophylla* in their aggressiveness. The more aggressive, the more efficient they are as predators. Observations on palms with strong colonies of *Oecophylla* support this contention. Some of these palms show good crops of nuts and no *Pseudotheraptus wayi* damage (which can be seen from the scars on the nuts), while others with equally strong *Oecophylla* colonies show a considerable, or rarely extreme, *Pseudotheraptus* damage and very few nuts. Data from five plantations over 3 years show that 17 318 palms which have only had small, passing or no *Oecophylla* colonies, yielded 311 895 nuts or an average of 18·1 nuts per annum whereas the 985 palms that had strong colonies of *Oecophylla* for at least 1 year previously, yielded 60 297 nuts or an average of 61·2 per palm. For full data see Vanderplank (1959a). These data show that the protection given by *Oecophylla* caused the crop to be increased over three times its previous level, but these data do not indicate how well *Oecophylla* controlled *Pseudotheraptus wayi*. In an experimental area of 800 palms that was treated with chemical insecticides, the average yields were for 15 years before treatment from 5·1 (1944) to 8·2 (1941) nuts/palm/annum, and after treatment 48·6 npa (control 6·9 npa). Of these palms 20% had permanent strong colonies of *Oecophylla* and these 160 palms yielded 3568 nuts (22·3 npa) the year before spraying, when the plantation as a whole only yielded 5·1 npa. Although *Oecophylla* were protecting the nuts so that a four-fold increase in yield was obtained, it was only 50% efficient assuming that the chemical treatment assessed by the *Vidaka* damage rate (Vanderplank 1958) only reduced *Pseudotheraptus wayi* damage 70% throughout the year. Other similar data are available which show that although *Oecophylla* affords a varying degree of protection, on an average it gives less than 50% control, and it must be remembered that only strong colonies that have remained in the palms for 2 years or more have been taken into account in these figures.

There is no doubt that *Oecophylla* must play a part in reducing the *Pseudotheraptus* population all over the plantation, since it will prey on the mobile adults, so palms in a plantation with numerous *Oecophylla* colonies should have less damage even though they do not harbour *Oecophylla* themselves. Observations support this contention. Yields in plantations which have no *Oecophylla* are very low, in most plantations well under 10 npa, and there is a correlation between the number of *Oecophylla* colonies and yield, the yield increasing with the percentage of *Oecophylla* present. Such differences may be due to soils and type of palms and not to the *Oecophylla*. However, in one control plot of 500 palms the percentage of palms with *Oecophylla* colonies has increased from 1952 with 19·8%, 1953 28·5%, 1954 39·8%, 1955 58·6% and yields have been 1953 6·1, 1954 8·1, 1955 16·9, 1956 27·6 npa. In this area then, a considerable increase in *Oecophylla* is correlated with a corresponding increase in yield. It is not known what this area would yield if there was no *Pseudotheraptus wayi* damage, but a near-by plot of

800 palms was increased from 5·1 to 8·2 to 48·6 npa by rather ineffective application of insecticides. These figures would again suggest that *Oecophylla* was not a very efficient means of controlling *Pseudotheraptus wayi*.

Oecophylla does not appear to prey on the weevil *Diocalandra frumenti* L. which can cause considerable loss of nutlets but it does appear to prey upon the larvae and adults of the borer *Lamoria* sp. that also can cause serious loss of nutlets. It is inimicable to *Polyrhacis* spp. which can also cause loss.

THE EFFECTS OF INSECTICIDAL SPRAYS ON *OECOPHYLLA*

Early in 1952 a coconut plantation of 120 acres was divided into six plots of about 20 acres each. A seventh plot of 10 acres, ½ mile away, was kept as a control. The three experimental plots were dusted with Agrocide-3 (active principle of 0·9% gamma B.H.C.) at various rates. The first three plots received ¼, ½ and 1 cwt of 0·9% lindane per acre every 14 days and the remaining three plots received the same amounts at monthly intervals. The dust was applied rather ineffectively by a Long Ashton duster. Table 5 summarizes the effect these dustings had on *Oecophylla* at the end of 4 months. The lowest dosage had weakened the colonies

Table 5. *Effect of insecticidal dust on* Oecophylla

Plot	Dose of Agrocide-3 (cwt/acre)	Interval between applications	Number of *Oecophylla* before dusting	Number after dusting	
A	¼	Monthly	197	815	Colonies considerably reduced in size
B	½	,,	235	105	
C	1	,,	176	6	The remaining colonies were very weak
D	¼	Fortnightly	152	43	
E	½	,,	212	3	
F	1	,,	255	Nil	Eradicated
Control	Nil	–	96	96	No obvious change

very considerably, and the highest dosage had eradicated them. In spite of reducing or eradicating *Oecophylla* and similarly reducing the populations of other species of ant, the homopteran populations increased considerably, demonstrating that they were not depending on ants for protection and keeping them free of contamination caused by moulds or fungi growing on their honeydew excretions.

Another experimental area of 800 palms was treated with three applications of 0·2% lindane dissolved in an oil base, and applied as a low volume air mist at monthly intervals and at 4 oz of lindane per acre (48 palms/acre). Before these applications there were seventy-eight colonies of *Oecophylla* in the palms, a month after the last application only three colonies remained, and these were on the windward edge of the plot. An area of 20 acres with 1120 palms was sprayed at monthly intervals with 50% wettable D.D.T. (80 p'p) at the rate of 4 lb/acre (42-48 palms/acre). Another plot of 12 acres was treated the same way at 10 lb/acre. In both plots the insecticide was applied as an air diluted mist. Ten monthly

applications were given and at the end of the year *Oecophylla* had been reduced from 187 to 78 colonies on the 20-acre plot and from 112 to 34 on the 12-acre plot. The applications of 4 oz of dieldrin per acre, applied as a 15% w/v solution in xylene was sufficient to eradicate all the *Oecophylla* from a 2-acre and a 10-acre plot. Four-monthly application of chlorinated camphene at the rate of 2 lb/acre has no significant effect on the numbers of *Oecophylla* colonies in the area. More than 300 acres have been sprayed monthly, bimonthly or quarterly for periods up to 3 years, and rates from ½ gal to 2 gal/acre/application, giving annual dosages as little as 6 lb/acre to as much as 25 lb/acre of 80 p'p D.D.T. made up a 10-DRDK formulation (Vanderplank 1959b). When the dosages did not exceed 15 lb acre/annum *Oecophylla* colonies increased in numbers and strength. With dosages between 16 and 20 lb/acre/annum there was no significant change in the numbers of colonies, but with dosages over 20 lb/acre/annum there was a decrease in the numbers of *Oecophylla* colonies and in the numbers of individuals in the colonies themselves.

Some insecticides or formulations have a marked effect on *Oecophylla* causing the whole colony to move to another site. It has already been pointed out that in an

Table 6. *Numbers of* Oecophylla *colonies moving from one nesting site to another per quarter*

Treatment	Number of colonies in area times the number of quarters observations were carried out	Number which moved to new site during quarters under observation	Percentage moving
None (control)	1980	7	0·36
Dust containing 0·9% lindane applied monthly at ¼ to 1 cwt/acre	519	465	89·6
The same applied at fortnightly intervals at ¼ to 1 cwt/acre	608	592	97·5
50% wettable D.D.T. at 4 lb/acre	187	85	45·5
50% wettable D.D.T. at 10 lb/acre	276	180	65·2
10-DRDK at 1 g/acre/month	416	20	4·8
10-DRDK at 2 g/acre/quarter	2838	147	5·2

untreated area a small percentage of the *Oecophylla* colonies will move to another site, particularly if they are heavily infested with predacious pests. Table 6 shows the effect of various insecticidal treatments on the movement of *Oecophylla* colonies. Treatment with lindane dust causes the most significant movement, but the difference between the two lindane treatments is not significant (as judged by the χ^2 test). Wettable D.D.T. caused significantly more movement than no treatment, or 10-DRDK, but significantly less than lindane. Even applications of 10-DRDK caused significantly more movement than no treatment at all, but significantly less than either lindane or wettable D.D.T. The difference between the two applications of 10-DRDK is not significant.

DISCUSSION

Although *Oecophylla* undoubtedly gives some protection to the coconut palm from *Pseudotheraptus wayi*, the amount of protection given varies with the individual colony and other ecological factors. Data are given showing that even strong colonies on an average only give 50% protection from *P. wayi* and none from the weevil *Diocalandra frumenti*. If *Oecophylla* could be induced to occupy 70 to 80% of all the palms at a low cost, this might be a compromise between expensive chemical control methods and no control at all. Way (1954) in Zanzibar and Phillips (1940) in the Solomon Islands have advocated using *Oecophylla* sp. to control *Pseudotheraptus wayi* or *Amblypelta cocophaga* China. Experiments and observations show that *Oecophylla* cannot thrive on honeydew alone and that a considerable amount of insect food is required to maintain the colony, so even if large areas of coconut plantations could be stocked with *Oecophylla*, there would be insufficient insect food to maintain such large populations. Various ways of increasing *Oecophylla* populations have been suggested from time to time. The most usual is that a large number of young colonies be reared in the laboratory and then transferred to coconut palms in the field. However, unless all antagonistic species of ants were prevented from foraging in the crowns, very few if any of the young *Oecophylla* colonies would survive. Even when other species of ants are destroyed and *Oecophylla* introduced into the ant-free palms, less than 5% of the colonies survive. This observation is from an experiment carried out on 200 palms in two locations. Since reproductive forms of all species are liberated frequently throughout the year, palms with no ants or only small colonies of *Oecophylla* or other species are open to competition from several young colonies of various species of ant, until finally one species is able to dominate. Another suggestion that has been made quite often is that existing colonies in the plantations should be encouraged by supplying them with honey or sugar in water. *Oecophylla* colonies do not take either honey or sugar in water very readily, but such solutions do encourage numerous other insects, particularly honeybees, wasps and other species of ant. The *Oecophylla* will capture a large number of honeybees and wasps at such sites, and it appears that the number of honeybees *Oecophylla* catch weigh more than the amount of honey supplied. Even if supplying syrup to *Oecophylla* colonies did eventually increase their numbers, I very much doubt whether this would be economical, owing to the high labour costs involved, and secondly such colonies would most probably become non-aggressive with small workers dominating, and so be of practically no value for controlling *Pseudotheraptus wayi*. Other methods for increasing the numbers of *Oecophylla* have been tried both in the Solomon Islands, Zanzibar and on the East African mainland. To date all methods have been complete failures.

The most promising method at the time of writing, is using an insecticidal formulation such as 10-DRDK, which although lethal to *Pseudotheraptus wayi*, *Diocalandra frumenti*, *Lamoria* sp., *Pheidole* sp. and other species of small ant, is not very harmful to either *Oecophylla* or *Apis mellifera*.

C J.A.E.

ACKNOWLEDGMENTS

My thanks are due to Dr W. J. Hall, C.M.G., M.C., Director of the Commonwealth Bureau of Entomology, and his colleagues for the identification of the many species of insects involved. This work would not have been possible without the assistance of my local staff who have carried out their duties conscientiously, often under difficult conditions, and this paper forms an account of our joint efforts. My thanks are also due to the Manager of Plantations.

SUMMARY

1. Some notes on the distribution of *Oecophylla* sp. are given.

2. Larvae failed to develop at 33·3° C but developed at 30° C, and the eggs failed to hatch at 16° C. It takes 25 days for the first workers to emerge at 28° C.

3. Colonies fed solely on honey produced mostly small yellow non-aggressive workers; those fed on insect food produced deep red large worker or soldier ants and were very aggressive.

4. Both insect food and sugars appear essential for the survival and reproduction of a colony.

5. Field experiments in rearing *Oecophylla* colonies are described.

6. All attempts to introduce a 'queen' *Oecophylla* to a 'queen-less' colony failed.

7. In the field *Oecophylla* colonies vary in colour, composition, feeding habits and aggressiveness; unless destroyed by antagonistic ants the life of a colony exceeds 5 years.

8. *Oecophylla* sp. are monogynous and the 'queens' move from nest to nest to oviposit.

9. The size of a colony was estimated by feeding with radio-phosphorus. It is estimated that the 'queen' must have been producing over 900 eggs a day and that the average life of the workers was between 68 and 140 days.

10. The most important antagonist of *Oecophylla* in Zanzibar is *Pheidole* sp.; two alien species of ant, *Anoplolepis longipes* and *A. custodiens*, established in parts of Zanzibar prey on *Oecophylla*. Most species of ant prey on the young 'queens'.

11. *Oecophylla* colonies are infested with a mimicking spider *Myrmarache* sp. and a pseudo-scorpion *Hansenius* sp. and other insects.

12. Some observations on the prey of *Oecophylla* are given. Unless the colony is numerically strong, it does not completely protect the palm from damage by *Pseudotheraptus wayi*.

13. A list of membracids tended by *Oecophylla* is given.

14. Solar movements influence the siting of leaf-nests more than the prevailing wind.

15. About 1% of colonies move to a new location during each year; these are usually heavily infested with arachnids.

16. *Oecophylla* is not selective in its choice of palms, but frequently occurs in groups; where all ant species were eradicated, re-colonization was at random.

17. Strong colonies of *Oecophylla* only give about 50% protection from *Pseudotheraptus wayi* damage and none from *Diocalandra frumenti* damage.

18. Insecticidal formulations containing lindane or dieldrin quickly reduce or eradicate *Oecophylla* from an area. The effects of some formulations of D.D.T. and other insecticides were also studied.

19. Some insecticides caused a considerable movement of *Oecophylla* colonies.

20. Although *Oecophylla* is a useful predator of *Pseudotheraptus wayi* and should not be destroyed, it is doubtful whether it could be used to obtain economical control of the pest.

REFERENCES

Brown, E. S. (**1954**). Entomological research on premature nutfall of coconut in British Solomon Islands. *Entomologist's Progress Report*, No. 1. (Typescript issued by Dept. of Agric., British Solomon Islands, Jan. 1955.)

Brown, E. S. (**1955**). Entomological research on premature nutfall of coconut in British Solomon Islands. *Entomologist's Progress Report*, No. 2. (Typescript issued by Dept. of Agric., British Solomon Islands, Jan. 1956.)

Lever, R. J. A. W. (**1935**). The green coconut bug, *Amblypelta cocophaga* China. *Brit. Solomon Is. Agric. Gaz.* **3,** 6.

Lever, R. J. A. W. & Phillips, J. S. (**1936**). Further experiments with *Amblypelta* and immature nutfall. *Brit. Solomon Is. Agric. Gaz.* **3,** 27.

Leach, R. (**1949**). Nutfall in the Solomons. *Progress, Lond.* **40,** 18.

O'Connor, B. A. (**1949**). Premature nutfall of coconuts in the British Solomon Islands Protectorate. *Fiji Agric. J.* **20,** 27.

O'Connor, B. A. (**1950**). Premature nutfall of coconuts in the British Solomon Islands Protectorate. *Fiji Agric. J.* **21,** 1-22.

Phillips, J. S. (**1940**). Immature nutfall of coconuts in the Solomons. *Bull. Ent. Res.* **31,** 295.

Steyn, J. J. (**1954**). The pugnacious ant (*Anoplolepis custodiens* Smith) and its relation to the control of citrus scales at Lataba. *Mem. Ent. Soc. S. Afr.* No. 3.

Vanderplank, F. L. (**1953**). Causes of coconut nutfall and gumosis. *Nature, Lond.* **172,** 315.

Vanderplank, F. L. (**1958**). Studies on the coconut pest *Pseudotheraptus wayi* Brown (Coreidae), in Zanzibar. I—A method of assessing the damage caused by the insect. *Bull. Ent. Res.* **49,** 559.

Vanderplank, F. L. (**1959a**). II—Some data of the yields of coconuts. *Bull. Ent. Res.* **50,** 135.

Vanderplank, F. L. (**1959b**). III—A selective residual insecticidal formulation and its effects on the ecology of the insect. *Bull. Ent. Res.* **50,** 151.

Way, M. J. (**1951**). An insect pest of coconuts and its relationship to certain ant species. *Nature, Lond.* **168,** 302.

Way, M. J. (**1953**). Studies on *Theraptus* sp. (Coreidae). The cause of the gumming disease of coconuts in East Africa. *Bull. Ent. Res.* **44,** 657.

Way, M. J. (**1954a**). Studies of *Oecophylla longinoda* Latreille. *Bull. Ent. Res.* **45,** 93-112.

Way, M. J. (**1954b**). Studies on the association of the ant *Oecophylla longinoda* (Lat.) with the scale insect *Saissetia zanzibarensis* Williams (Coccoidae). *Bull. Ent. Res.* **45,** 113-34.

A CONTRIBUTION TO THE FEEDING BIOLOGY OF *MITOPUS MORIO* (F) (PHALANGIDA)

By J. PHILLIPSON

Department of Zoology, Durham

(With 1 Figure in the Text)

It is evident from the work of O'Brien (1947) and Todd (1950) that phalangids are important predators in the habitats they occupy. In the present work, using *Mitopus morio* (Fabricius) adults, an attempt has been made to determine (1) the type of food eaten, (2) the method of capturing food, (3) the time of feeding, (4) the percentage assimilation of food in the laboratory and (5) the energy transfer occurring between prey and predator in the field.

THE FOOD OF *MITOPUS MORIO*

Of 1367 faecal pellets collected in the laboratory over the whole breeding season, from 174 males and 159 females taken in the field and given no food in the laboratory, only three contained plant remains. The plant materials were in such small quantity that they may have been eaten accidentally or were possibly the gut contents of animals eaten by *Mitopus*. Many pellets contained fragments of arthropod skeletons. It can be concluded, therefore, that *M. morio* feeds mainly, if not wholly, on animal material in nature.

Individuals of *M. morio* were kept separately in circular glass dishes $15 \times 7{\cdot}5$ cm sealed by a glass plate. The bottom of each dish was covered by filter paper kept moist with water from an inverted 2×1 in. glass tube. Temperatures ranged between 12 and 18° C. The animals were starved for 24 h after capture. Thirty-three different kinds of potential food animal collected from the same habitat as *M. morio* were offered. A group of ten individuals of each species was tested as food, one live animal at a time being introduced into each dish. Table 1 shows that a variety of animals was eaten. Animals much larger than *Mitopus* or protected by a very hard casing or much mucus were attacked during the experiments, but none were killed. Table 2 shows that animals of suitable texture and within the correct size-range were readily eaten (8 out of 10); wingless forms were taken more quickly than winged.

CAPTURE OF PREY

The movements shown by *M. morio* when capturing prey were filmed at 64 frames/sec using a 16 mm Ciné Kodak Special. The prey was attacked as soon as the phalangid made physical contact with it. The following description begins where physical contact was made. The drawings were based on individual frames. In Fig. 1*a* the *Mitopus* was stationary and a suitable prey animal, a *Sciara* sp. (Diptera, Mycetophilidae) approached. Contact was made with the second walking

leg of the phalangid (Fig. 1*b*) which then reacted by drawing all the legs inwards, thus narrowing the escape routes available to the *Sciara*. Simultaneously, the fly was pulled towards the mouthparts by the walking legs (Fig. 1*c*) and delivered to

Table 1. *Food animals offered to* Mitopus morio

Ten individuals of each species were offered

	Taken	Rejected
ANNELIDA		
Enchytraeidae <1 cm long	5	5
Lumbricidae <1 cm long	3	7
ISOPODA		
Trichoniscus sp.	5	5
Philoscia sp. ~1 cm long	0	10
COLLEMBOLA		
Orchesella sp.	6	4
DIPLURA		
Campodea sp.	9	1
DERMAPTERA		
Forficula sp. ~2 cm long	1	9
HEMIPTERA		
Philaenus sp.	9	1
Jassidae	9	1
Microlophium sp. (winged)	9	1
Microlophium sp. (wingless)	9	1
LEPIDOPTERA		
Microlepidoptera	9	1
Pieris sp. (larva <2 cm long)	9	1
COLEOPTERA		
Megasternum sp. <0·5 cm long	9	1
Loricera sp. >1 cm long	0	10
Carabidae (larva <1 cm long)	9	1
Philonthus sp. >1 cm long	2	8
Otiorhynchus sp. <0·5 cm long	1	9
HYMENOPTERA		
Chalcidae	8	2
Formica sp.	0	10
DIPTERA		
Sciara sp.	9	1
Scopeuma sp.	10	0
Lucilia sp.	4	6
CHILOPODA		
Lithobius sp. >1 cm long	0	10
Lithobius sp. <1 cm long	8	2
DIPLOPODA		
Cylindroiulus sp. >1 cm long	0	10
Iulus sp. <0·5 cm long	7	3
ARANEIDA		
Meta sp. <1 cm long	8	2
Meta sp. >1 cm long	1	9
ACARINA		
?	7	3
PHALANGIDA		
Oligolophus sp.	9	1
GASTROPODA		
Cothlicopa sp.	0	10
Arion sp. <0·5 cm long.	0	10

Table 2. *Time taken for consumption of the food animals most readily eaten*

Wingless food	Average time taken for capture (days)	Winged food	Average time taken for capture (days)
Philaenus sp.	1·6	Chalcidae	2·8
Pieris sp. (larva)	1·6	*Scopeuma* sp.	3·1
Carabidae (larva)	2·1	Microlepidoptera	3·2
Lithobius sp. <1 cm long	2·2	*Sciara* sp.	3·3
Megasternum sp.	2·7	*Microlophium* sp. (winged)	3·5
Campodea sp.	2·8	Jassidae	4·0
Oligolophus sp.	2·9		
Mean 2·3 ± 1·5		Mean 3·3 ± 2·4	

the fully extended clawed pedipalps (Fig. 1*d*). The *Sciara* was seized by the chelicerae (Fig. 1*e*) and released by the pedipalps (Fig. 1*f*) which were used now only to reposition the fly from time to time. The chelicerae held the *Sciara* clear

of the ground and, working in opposition to each other, alternately pushed and tore at it. This sequence took 1·16 sec. The capture of food was filmed with different individuals and was always similar in method although the initial point

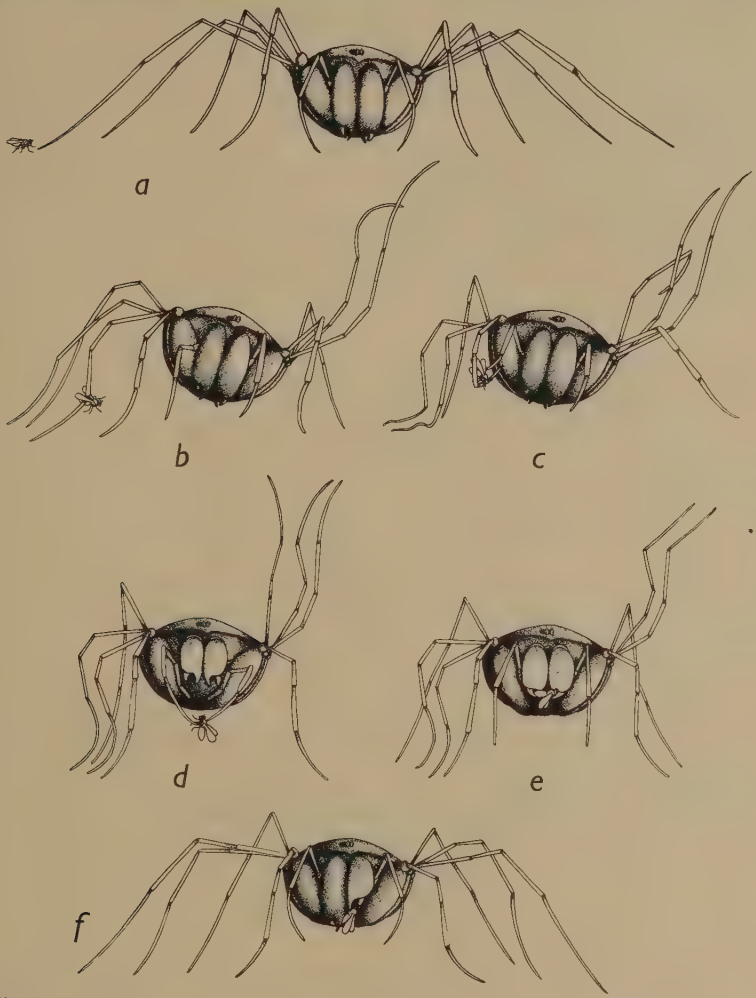


Fig. 1. The sequence of movements made by *Mitopus morio* when capturing its prey.

of contact between phalangid and food varied, as did the time taken for such a sequence.

TIME OF FEEDING

It was difficult to assess directly the times of maximum feeding activity in the field because of the relatively few animals seen with food, but it was determined

indirectly in the laboratory. Twenty-five animals of each sex were starved for 48 h so that all chitinous food remains were voided. Each was then fed a single *Sciara*. Faecal pellets were collected every three hours and examined for chitin. The chitin appeared 19·7±3·2 h after feeding in females, and 15·5±1·5 h in the case of males. In a second experiment twenty-five animals of each sex were collected in the field at 2300, 0500, 1100 and 1700 h G.M.T. during a single day (7-8 September). Every three hours faecal pellets were collected and examined for chitin and the time at which it appeared after capture noted (Table 3). The total volume of faeces produced by each group could be calculated because the relatively firm pellets approximate in shape to an ellipsoid, the volume being estimated by the formula $\frac{4}{3}\pi ab^2$ where a and b are the radii of conjugate diameters of an ellipsoid. Knowing the time taken for chitin to appear after feeding in the control it was possible to calculate the time of day when feeding occurred in the

Table 3. *Time of feeding in the field and volume of faeces produced in* 24 *h*

Hours of darkness 1915–0500 h G.M.T., 7-8 September 1957

	Females				Males			
Time of collection (G.M.T.)	2300	0500	1100	1700	2300	0500	1100	1700
Time of appearance of chitin (hours after capture)	10·2 ±6·0	9·25 ±4·3	4·4 ±3·7	7·0 ±5·1	9·0 ±2·3	10·4 ±4·25	11·0 ±3·3	13·0 ±6·1
Longest period in which feeding could have taken place (G.M.T.)	0400 to 2230	1100 to 0200	1230 to 0230	2000 to 1230	1230 to 2000	1800 to 0530	0130 to 1100	0700 to 2200
Shortest period in which feeding could have taken place (G.M.T.)	1030 to 1600	1730 to 1930	1900 to 2000	0230 to 0600	1530 to 1700	2100 to 0230	0430 to 0800	1000 to 1900
Volume of faeces in first 24 h after capture (mm^3)	197·4	227·2	228·1	194·3	26·7	68·0	56·3	24·6

field. Results are given in Table 3. It is evident that food was taken at all times of the day but the greater total volume of faeces produced by the groups feeding during the hours of darkness shows that feeding activity increased at night.

ASSIMILATION OF FOOD

(*a*) *In the laboratory*

Richman (1958) used the equation:

Assimilation = energy of growth + energy of respiration.

Experiments were made on adult *Mitopus morio* of both sexes to determine the percentage of ingested food that was assimilated. Dry weights were determined by heating at 110° C to a constant weight. When a *Calocoris* sp. (Heteroptera) was eaten, green faecal pellets were produced. This provided a convenient way of calculating the exact weight of faeces produced from a known weight of ingested food. After eating one *Calocoris* all green faeces were voided within 36 h. Since growth would be negligible in so short a time, assimilation was regarded as energy

of respiration. Table 4 shows the average amount of assimilation expressed as a percentage of food ingested. Foods eaten in later experiments failed to colour the faeces distinctively, and an indirect method of assessing assimilation was necessary. This entailed the use of *Calocoris* as a standard. Each experiment lasted 24 h and growth was assumed to be negligible. Thus, in terms of dry weight:

food eaten = food − food not eaten;
non-assimilated food = gain in weight of *Mitopus* after 24 h + food not eaten + faeces;
food assimilated = food eaten − non-assimilated food.

Table 5 shows the summarized results for *Calocoris* sp. These measurements approximate closely enough to the results of the direct method (Table 4) to justify

Table 4. *Amount of food* (Calocoris *sp.*) *assimilated*

	Males			Females		
	Dry weight of prey (mg)	Dry weight of food consumed (mg)	Dry weight of faeces (mg)	Dry weight of prey (mg)	Dry weight of food consumed (mg)	Dry weight of faeces (mg)
1	0·61	0·37	0·33	1·22	0·90	0·61
2	0·94	0·35	0·31	0·73	0·49	0·48
3	1·49	0·21	0·10	1·29	0·94	0·46
4	0·78	0·38	0·25	0·80	0·56	0·41
5	1·32	0·31	0·18	0·68	0·47	0·38
6	0·66	0·47	0·15	1·25	0·89	0·46
7	1·43	0·30	0·08	1·04	0·56	0·23
8	1·43	0·60	0·15	1·17	0·84	0·32
9	1·31	0·26	0·18	1·15	0·95	0·59
10	1·44	0·80	0·31	1·13	0·71	0·32
Total	11·41	4·05	2·04	10·46	7·31	4·26
Average percentage assimilated of food consumed		49·4 (Range 25·0-89·2)			41·7 (Range 38·0-98·0)	

the use of the indirect method when animals such as *Scopeuma* sp., *Philaenus* sp., *Oligolophus* sp., and *Pieris* sp. larvae were used as food. The summarized results in Table 5 show that the percentage of ingested food assimilated was, in all but two cases, between 40 and 50%, with an average value of 47%.

(*b*) *In nature*

For this estimate, use was made of data on faecal pellets from the eight groups of twenty-five animals recorded in Tables 3 and 6. The mean number of pellets per animal per 24 h was $2{\cdot}68 \pm 0{\cdot}78$ in females and $2{\cdot}54 \pm 0{\cdot}91$ in males. The mean volume of a single pellet was 3·2 mm^3 for females and 0·7 mm^3 for males. Thus a daily average of 8·58 mm^3 of faecal matter per female and 1·75 mm^3 per male was produced. Further experiments showed that the average wet weight of 1 mm^3 of faeces was 0·13 mg for both sexes. Thus, an average female *Mitopus morio* produces 1·12 mg wet wt (0·29 mg dry wt) of faeces daily and an average

male 0·23 mg wet wt (0·06 mg dry wt). The laboratory experiments on assimilation showed that 47 % of the food eaten is assimilated, the remainder being voided as faeces. Thus, an average female eats 0·55 mg dry wt of food daily, of which 0·26 mg is assimilated. A male eats 0·11 mg dry wt of food daily and assimilates 0·05 mg of this.

Table 5. *The amounts of food assimilated when various animals were used as food*

All weights are dry weights correct to two decimal places. Each figure is the mean of ten experiments; the range is given in parentheses.

Food animal	1 Gain in wt (mg)	2 Wt of food (mg)	3 Wt of food not eaten (mg)	4 Wt of faeces (mg)	5 Wt of food not assimilated (mg) 1+3+4	6 Wt of food assimilated (mg) 2−5	7 Wt of food eaten (mg) 2−3	Amount of food assimilated as a percentage of food eaten	Amount of food eaten as a percentage of food captured
MALES									
Calocoris sp.	0·15 (0·0-0·43	1·16 (·61-1·5)	0·72 (·19-1·26)	0·09 (·05-·18)	0·96 (·39-1·36)	0·20 (·02-·57)	0·44 (·24-·81)	45·0	38·1
Scopeuma sp.	0·21 (·07-·31)	3·19 (1·67-4·04)	2·72 (1·16-3·75)	0·08 (·05-·10)	2·99 (1·43-4·01)	0·20 (·06-·60)	0·47 (·38-·76)	42·6	14·9
Philaenus sp.	0·63 (·23-·93)	3·99 (1·79-6·1)	2·53 (1·17-4·56)	0·08 (·05-·23)	3·24 (1·48-4·98)	0·75 (·29-1·4)	1·46 (·62-2·38)	51·3	36·5
Oligolophus sp.	0·07 (0·0-·20)	2·15 (1·95-2·75)	1·89 (1·06-2·75)	0·07 (·03-·15)	2·03 (1·23-2·78)	0·12 (·02-·68)	0·26 (·21-·69)	46·0	12·1
Pieris sp. (larva)	0·26 (·07-·44)	1·53 (·57-3·78)	0·84 (·15-1·94)	0·08 (·03-·18)	1·19 (·58-2·4)	0·35 (·07-1·38)	0·69 (·36-1·84)	50·0	45·1
Means								47·0	27·6
FEMALES									
Calocoris sp.	0·64 (0·0-1·0)	1·91 (·71-2·66)	0·43 (·10-1·65)	0·13 (·10-·20)	1·20 (·20-2·13)	0·72 (·15-·86)	1·48 (·61-2·18)	48·1	77·4
Scopeuma sp.	0·87 (0·0-1·63)	2·58 (2·07-3·23)	0·73 (·49-1·09)	0·20 (·03-·38)	1·79 (·91-2·64)	0·78 (·01-2·15)	1·85 (1·0-2·47)	42·0	71·8
Philaenus sp.	0·79 (0·0-1·76)	2·96 (1·9-3·59)	1·04 (·63-1·66)	0·23 (·03-·56)	2·06 (1·46-2·9)	0·89 (0·24-2·13)	1·92 (1·16-2·23)	46·8	64·8
Oligolophus sp.	0·51 (·04-·96)	2·84 (1·21-4·32)	1·15 (·37-2·03)	0·36 (·08-·8)	2·02 (·85-3·48)	0·82 (·22-1·32)	1·49 (·52-2·6)	55·2	52·3
Pieris sp. (larva)	0·84 (·31-1·59)	3·73 (2·97-4·09)	1·39 (·55-2·63)	0·33 (·20-·54)	2·56 (1·8-3·66)	1·17 (·64-2·14)	2·33 (1·16-3·6)	50·0	62·5
Means								47·0	66·1

DISCUSSION

The food of harvest-spiders is very varied. Kästner (1926) and Bristowe (1949) state that plant materials are occasionally taken as food. Bristowe (1949), Sankey (1949), Todd (1949, 1950) and Immel (1954, 1955), report both living and dead animals as food. Immel (1953, 1954) has shown that plant starches are rejected as food by *Nemastoma quadripunctatum*. The present work on *Mitopus morio* shows that plants are not eaten. *M. morio* eats only animals, and general observations indicate that only living or recently dead species of a certain size and texture are eaten readily. *M. morio* captured wingless prey more quickly than winged forms.

The capture of food by *M. morio* after physical contact was made, differs only in detail from previous descriptions of the method by which other harvest-spiders capture food (Stipperger 1928, Kästner 1935, Roters 1944, Pabst 1953, Immel 1954, 1955). However, authors before Immel (1953) implied that phalangids are active hunters, using the pedipalps and walking legs as chemosensory organs to locate the food. Immel (1953, 1954) showed that *Nemastoma quadripunctatum* had poor vision, very little sense of smell and was incapable of following a trail of meat

Table 6. *Average number and volume of faecal pellets per individual* Mitopus morio

	Females				Males			
Time of collection (G.M.T.)	2300	0500	1100	1700	2300	0500	1100	1700
Volume of faeces per twenty-five animals (mm^3/24 h)	197·4	227·2	228·1	194·3	26·7	68·0	56·3	24·6
Total number of faecal pellets per twenty-five animals per 24 h	64	62	75	67	47	74	80	53
Average number of faecal pellets per individual per 24 h		2·68 ±0·78				2·54 ±0·91		
Average volume of faeces per individual (mm^3/24 h)		8·58				1·75		

extract. It did not respond to food until physical contact had occurred. *Mitopus morio* showed the same reaction. This probably indicates that the Nemastomatidae and Phalangiidae are not active hunters, but remain stationary with the legs radiating round the body so that, collectively, they function in much the same way as a spider's web, their legs being very responsive to tactile stimulation. This does not mean that phalangids are completely sedentary animals, for they can move from one site to another.

Whatever the method of capturing food, the present work shows that feeding occurs at any time of day or night, thus agreeing with Stipperger (1928). Pickard-Cambridge (1890), Ruhm (1926), Kästner (1931), O'Brien (1947), Todd (1949) and Sankey (1949, 1956) all pointed out that although phalangids are mainly active at night they are not strictly nocturnal. The present work corroborates this by showing an increased food intake during the hours of darkness. Increased activity at night can be explained by the humidity responses of phalangids. Todd (1949) showed that many harvest-spiders prefer high humidities. At night, relative

humidity near the ground and in herbage increases, thereby extending the range of the phalangids. A vertical spreading out of the harvest-spiders plus the fact that many day-flying insects shelter in the herbage at night will increase the number of prey animals relative to the number of harvest-spiders. Thus, the opportunities for chance encounters between phalangid and food will be increased and could explain the greater food uptake during the hours of darkness.

The scale of energy transfer between food and phalangid was estimated from the percentage assimilation of ingested food in the laboratory and the quantity of food eaten in the field. Although determined by an indirect method, it has an advantage over measures of assimilation calculated from respiratory rates, because it takes into account the daily fluctuations of temperature. Gibb (1957) gives the calorific value of 'mixed insects' as 5·82 kcal/g dry matter. Using this figure, it was calculated that a female *M. morio* of 50 mg daily ingests food with a calorific value of 3·2 cal; of this 1·5 cal are assimilated and thus lost to the system, and 1·7 cal are returned to the soil as faeces. A male *M. morio* of 23 mg daily ingests food with a calorific value of 0·64 cal, of which 0·29 cal are assimilated and 0·35 cal are returned to the soil as faeces. No explanation is offered for the difference in metabolic rate shown by males and females.

A factor not yet considered in discussing energy transfer between food and phalangid is the food not eaten and thus left on the soil as fragmented remains. It is not possible to make an exact estimate of the quantities involved because the size of food animals varies. However, if the weight of food captured in nature is within the same range as that used in laboratory experiments on assimilation, an estimate can be made. It is evident from Table 5 that an average of 33·9% of the food captured by females and 72·4% of that captured by males is left as fragmented remains. The calorific equivalents of these figures are 1·64 cal for females and 1·68 cal for males. Thus, the daily 'total energy budget' for a 50 mg female *M. morio* is as follows: the calorific value of food captured is 4·84 cal, of which 1·5 cal are assimilated, 1·64 cal are left as food remains, and 1·7 cal are returned to the soil as faeces. Similarly, for an adult male *M. morio* of 23 mg the calorific value of food captured per day is 2·32 cal, of which 0·29 cal are assimilated, 1·68 cal are left as food remains and 0·35 cal as faeces.

ACKNOWLEDGMENTS

Thanks are due to Prof. J. B. Cragg for helpful discussion during the course of the work and also for comments on the preparation of the manuscript.

SUMMARY

1. *M. morio* eat a variety of animals, mostly arthropods living or recently dead. Animals much larger than the phalangid or with a protective cover of much mucus or hard exoskeleton were rejected. Plant materials were not eaten in nature.

2. *M. morio* detects food only by physical contact with it. The walking legs function in a similar way to a spider's web.

3. *M. morio* fed at all times of day but more during darkness. An average of 47% of all food eaten was assimilated.

4. In nature, the average calorific value of food captured daily by a 50 mg female *M. morio* was 4·84 cal, of which 1·5 cal were assimilated and 3·34 cal were returned to the soil as faeces or non-ingested food remains. A male *M. morio* of 23 mg daily captured food with an average calorific value of 2·32 cal, of which 0·29 cal were assimilated and 2·03 cal were returned to the soil.

REFERENCES

Bristowe, W. S. (**1949**). The distribution of harvestmen (Phalangida) in Great Britain and Ireland, with notes on their names, enemies and food. *J. Anim. Ecol.* **18,** 100-14.

Gibb, J. (**1957**). Food requirements and other observations on captive tits. *Bird Study*, **4,** 207-15.

Immel, V. (**1953**). Zur Physiologie des chemischen Sinnes von *Nemastoma quadripunctatum* (Opiliones, Dyspnoi). *Naturwissenschaften*, **40,** 609-10.

Immel, V. (**1954**). Zur Biologie und Physiologie von *Nemastoma quadripunctatum* (Opiliones, Dyspnoi). *Zool. Jb.* (*Syst*), **83,** 129-84.

Immel, V. (**1955**). Einige Bermerkungen zur Biologie von *Platybunus bucephalus* (Opiliones, Eupnoi). *Zool. Jb.* (*Syst*), **83,** 475-84.

Kästner, A. (**1926**). Opiliones, in **Schulze, P.,** *Biologie der Tiere Deutschlands*. Lief. 18, Teil 19. Berlin.

Kästner, A. (**1931**). Biologische Beobachtungen an Phalangiden. *Zool. Anz.* **95,** 293-302.

Kästner, A. (**1935**). Opiliones Sundervall-Weberknechte, in **Kükenthal & Krumbach,** *Handbuch der Zoologie*, **3** (9), 300-84. Berlin.

O'Brien, M. V. (**1947**). Observations upon the ecology of the Phalangida of the Chicago area. *Bull. Ecol. Soc. Amer.* **28** (4), 61.

Pabst, W. (**1953**). Zur Biologie der mitteleuropäischen Troguliden. *Zool. Jb.*(*Syst*), **82,** 1-46.

Pickard-Cambridge, O. (**1890**). On the British species of Phalangidea or harvestmen. *Proc. Dorset. Nat. Hist. Fld. Cl.* **11,** 163-216.

Richman, S. (**1958**). The transformation of energy by *Daphnia pulex*. *Ecol. Monogr.* **28,** 273-91.

Roters, M. (**1944**). Observations on British harvestmen. *J. Quekett Micr. Cl.* (4) **2,** 23-5.

Rühm, J. (**1926**). Ueber die Nährung von *Phalangium* L. *Zool. Anz.* **68,** 154-8.

Sankey, J. H. P. (**1949**). British harvest spiders. *Essex Nat.* **28,** 181-91.

Sankey, J. H. P. (**1956**). How to begin the study of harvest spiders. *Countryside*, **17,** No 9, 1-8.

Stipperger, H. (**1928**). Biologie und Verbreitung der Opilioniden Nord-Tirols. *Arb. zool. Inst. Univ. Innsbruck*, **3,** 12-79.

Todd, V. (**1949**). The habits and ecology of the British harvestmen (Arachnida, Opiliones), with special reference to those of the Oxford district. *J. Anim. Ecol.* **18,** 209-29.

Todd, V. (**1950**). Prey of harvestmen (Arachnida, Opiliones). *Ent. Mon. Mag.* **86,** 252-4.

THE DISTRIBUTION OF INSECTS AT LOW LEVELS IN THE AIR

By L. R. TAYLOR

Department of Entomology,
Rothamsted Experimental Station, Harpenden, Herts.

(With 10 Figures in the Text)

Migrating insects are often recorded as flying at specific heights, usually a few feet above the ground; migrant butterflies are specially apt to give the impression of flying at a selected level. But the same impression is also gained by observers of other kinds of insects. How much the judgment with small insects is affected by the height of the observer, 5-6 ft, is a matter for conjecture. In contrast to such impressions, many small insects have been caught at heights up to 15 000 ft and such insects can hardly be supposed to have chosen to fly at any specific height. The distinction between a selected height of flight and one imposed to some extent by forces outside the control of the insect is important in developing a rational view of insect movement, including the distances travelled.

Agricultural entomologists studying crop infestations have collected most of the existing information on low-level flight, so the species studied are few and all are small. Nevertheless, workers have suggested that given species mostly fly at specific heights and that different species, even of such a physically homogeneous group as aphids, fly at different heights. If this suggestion is correct, it implies a different kind of distribution of the same insects at low and at high levels. Johnson (1957a) has shown from trapping records at high levels that insect density diminishes continuously and regularly as height increases, which suggests that distribution is determined by factors outside the immediate control of the insect. The ranges of height he dealt with were: 200 to 5000 ft (data from Glick 1939); 80 to 1500 ft (data from Hardy & Milne 1938); 10, 177 and 277 ft (data from Freeman 1945); 50 to 2000 ft and a small amount of material at 10, 50, 500 and 1000 ft (data of Johnson 1957a). Although these records often extend up to very high levels, they are relatively few near to the ground.

Small insects must frequently fly in wind speeds well above their own low flight speeds even at low levels. For example, the flight speed of thrips (T. Lewis, unpublished), aphids and psocopterons (Taylor, unpublished), and probably many other small insects, is less than 1 m/sec. The air speed at Kew, a sheltered inland station in England, in 1937 exceeded 1 m/sec at 10 m for almost 90% of the time. At 2 m it would exceed 0·78 m/sec for 90% of the time (*see* Gregory 1945); in other words, the wind above 2 m is higher than the flight speed of many small insects for most of the time. Johnson (1954) showed conclusively that migratory aphids fly mainly in windy weather. This might be expected to lead to some kind of continuity of density distribution at all levels. I have therefore re-examined the

evidence about the distribution of insect density in relation to height up to about 30 ft to see whether or not such a discrepancy between high-level and low-level flight does exist. Insect density has rarely been measured directly at these levels and it is necessary to transform the insect catches to density, somewhat arbitrarily, before the main object of the analysis can be dealt with. This object is to try to establish whether there are maximum densities of insects at particular heights specific to individual species. This would demonstrate height selection completely controlled by the insect. Alternatively, if the height distribution continuously diminishes, it probably results from meteorological factors beyond the immediate control of the insect, although it may still be affected in part by the insect's size, flight capabilities and behaviour.

THE ESTIMATION OF INSECT DENSITY

Information about the number of insects in the air is obtained by trapping. The traps used are of four kinds; attractant, suction, impaction and nets. Attractant traps are useless for this kind of comparison because the insects' sensory responses are not sufficiently understood to interpret the results so obtained. Enough suction traps have not been used at these levels to provide a full record (see p. 58); only impaction traps, such as sticky boards and screens, and suspended nets do this. Non-selective water trays, which act largely as impaction surfaces, have been used simultaneously with sticky traps (Lewis 1959). These traps depend for their sampling power upon the wind and, except at very low wind speeds, may be expected to sample a reasonably constant proportion of the insects contained in the air blown against them (Johnson 1950). It is from catches obtained in this way that all previous conclusions about height of flight at low levels have been drawn.

The trap catch represents the quantity of flow of insects and this is the product of rate of flow, *i.e.* the wind speed, and the insect density, *i.e.* the number of insects per unit volume of air. Thus, the catch of each trap must be divided by the wind speed across it to find the insect density. This requires a wind speed at each trap height, in other words a profile of wind speed against height, but since wind speed profiles have rarely been measured when trapping was in progress, they have to be estimated. The general profile relating wind speed to height is well established by experiment. It is a statistical curve, constant as a mean value over a period of time, but not necessarily so in individual examples; trapping records are also taken over long periods.

The frictional drag of the ground slows the air in contact with it, and the air in turn transmits the braking effect upwards through adjacent air layers. A profile of increasing relative wind velocity with height is produced; this has a characteristic mean shape irrespective of the absolute wind velocities involved. The rate at which the braking effect moves upwards depends upon the roughness of the ground; also, as the vegetation grows, so the ground level is in effect raised and the relative velocity profile is affected.

The wind profile can be almost equally well described by several expressions; the

form used here was derived especially for irregular or deep ground cover (Sutton 1953, p. 239). It is:

$$U_r = \frac{1}{K}\left\{\log_e (Z_r - \bar{d}) - \log_e Z_o\right\} \quad (1)$$

where U_r = relative velocity at height Z_r
K = von Kàrmàn's constant = 0·4

$\bar{d}$ and Z_o are constants for each occasion which, in general, increase as the ground cover becomes deeper and rougher respectively. It is usually impossible to know the ground cover precisely from information provided by authors primarily concerned with insect numbers, but the height of vegetation can often be guessed. Fortunately, changing these values does not greatly change the wind speed profile. The major effect is produced by the sum of $\bar{d}$ and Z_o, which raises the whole profile to a higher level as it increases, so that the theoretical profile comes to zero at the point $(\bar{d}+Z_o)$, and this is related to the level of the plants. In practice the wind is obviously not zero at this point and Fig. 1*d* shows measurements (kindly provided by Dr H. L. Penman from unpublished material) along with a fitted curve and the appropriate, eye-fitted, tail down to zero velocity at zero height, inside the vegetation. The effect of using two different expressions for the velocity profile, fitted by Dr Penman to data of Jensen (1954), is shown in Fig. 1 *b* and *c*. Fig. 1 *a* and *b* also compare the effect of using two different sets of values for $\bar{d}$ and Z_o in the same expression. In each example the tail down to zero height was drawn in by eye.

Fig. 1 *e* to *j* give most of the profiles used here. Those omitted resemble one or other of those given. The region of doubtful applicability, the steep portion of the curve and the fitted tail, never extends above 3-4 ft. Altering the form of profile would have little effect on the profile above this level. Although profiles approximately suitable for any particular set of data can be found, they obviously cannot be relied on absolutely; hence, unquestionable conversions cannot be made. A mean wind profile could be applied to all the data, but this would lose precision. Some authors have examined catches of several species of insect and this allows a different approach to be adopted. The wind profile is a property largely of the site and time of measurement, for $\bar{d}$ and Z_o may change with the season. But the same wind profile must apply to all kinds of insects caught on the same occasions in the same traps. Also, if a system of traps is operated in the same situation for several consecutive years, it is reasonable to expect that the same wind profile will apply to each separate year and individually to each species caught.

The curves for catches of insects plotted against height are of several shapes; rising curves, falling curves, and curves that rise and then fall to give a maximum catch at different heights in different instances. In contrast, all Johnson's data for density give a linear graph for log density × log height over short distances. When a suitable wind profile can be found to convert the curve for catch to a linear log density × log height curve for one species, the same wind profile should convert the catch curves for other species from the same traps equally well; but this will

happen only when the wind profile is correct and when the linear log density × log height relation is valid. If each species has its own particular intrinsic height

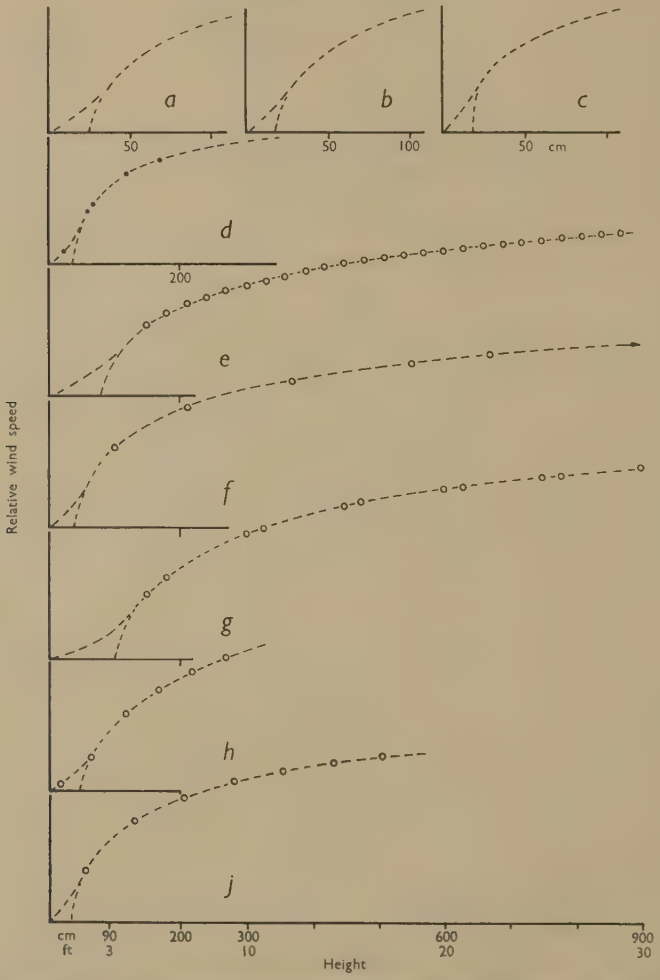


Fig. 1. Wind profiles. *a*, *b*, *c*, three alternative profiles fitted to data by Jensen (1954) for 20 cm crop: *a*, log profile, $d = 20$; $Z_o = 5{\cdot}5$; *b*, log profile, $d = 10$; $Z_o = 8$; *c*, power law profile, $\frac{U_1}{U_2} = \left[\frac{Z_1 - 18}{Z_2 - 18}\right]^{0{\cdot}32}$; *d*, log profile $d = 25$: $Z_o = 9{\cdot}5$ fitted to data by Penman for 60 cm wheat crop; *e*, *f*, *g*, *h*, *j*, log profiles used in converting catches to density: *e*, Shands *et al.* (1956), Wisconsin; *f*, Riggert (1931); *g*, Shands *et al.* (1956), Maine; *h*, Profft (1939); *j*, Körting (1931).
•, measured wind velocities; ○, windspeeds used in conversions.

distribution, the resulting density profiles are unlikely to be linear by coincidence. To avoid selecting one particular species upon which to base this operation, the argument can be taken a step further. If the linear log density × log height relation

is correct, it follows that a geometric mean catch of all species at each height should also be converted to give a linear log density × log height graph: a density gradient for 'all insects'. This is because the straight line log density × log height profiles can be added together to give another straight line. Again the operation is unlikely to produce a straight line by the addition of several curves each with an intrinsic property of its own, except by coincidence. And a final test is to convert the catches obtained in 1 year by using the wind profile calculated in other years for the same set of traps. Fortunately, this can be done. Such a process could not be regarded as proving that the linear log density × log height curve absolutely describes the data; a slight bend in the curve would not be detected because of inevitable errors in the catches. But it would demonstrate that the conversion is valid in principle, especially when the resulting wind profiles are not unreasonable and when the resulting density profiles bear some relation to the physical and biological characteristics of the insects concerned.

This is the method adopted. The wind profiles were selected, with due regard for what is known about the ground cover, to attempt to transform the geometric mean catch for all species to a linear log density × log height profile. The same wind profile was then applied to each species separately, and once to a separate set of data from the same site but in a different year. The success of the conversions may be judged by the figures. The reasonableness of the values for $\bar{d}$ and Z_o used is then discussed, along with the density profiles produced.

THE DATA ON VERTICAL DISTRIBUTION

Wolfenbarger (1946) fitted curves to several sets of records of insects caught at different heights. Some of these consist of only three points, too few for satisfactory conversion, the data of Gaines & Ewing (1938) are not given in full in the original paper, those of Goodwin (1942) were obtained by trapping mosquitoes at resting sites and are not a dispersal record, and those of Dominick (1943) were obtained on sets of traps in three vertical series, each with only three separate points. There remains the work of Profft (1939) and Körting (1931) which is suitable for analysis and deals with more than one species. The data of Riggert (1931) relate to one species only and are mentioned later. There are now additional records. The catches by Shands, Simpson & Dudley (1956) over many years and in different places provide excellent material. Nowak (1951) trapped *Myzus persicae* Sulz. at six heights in five situations for a season, but the catches were too small and variable to draw conclusions from them. Davis, Landis & Gibson (1954) collected aphids at four heights but did not publish the full data. Broadbent (1948) did extensive trapping of aphids, but only at three heights. There are some results from suction traps. Full data for catches are given in the original papers and are not reproduced here (see Appendix). Diagrams are given of the catches and the densities estimated from them; the value of $\bar{d}$ and Z_o for the wind-speed profile is always given. Densities are given on a log × log scale, but in the first example they are converted back to the arithmetic scale for comparison with the catch curves. The means used for several species or groups are geometric; this gives more

equal weight to each group, for one group is often much commoner than the others.

(*a*) *Data of Körting* (*1931*)

Thrips (*Limothrips cerealium* Hal. and *Haplothrips aculeatus* Fab.) and frit fly (*Oscinis frit* L.) were collected on a post, 6 cm square and 5·5 m (18 ft) high, covered with adhesive-coated parchment, from 19 June to 14 October 1929 on an experimental plot at Königsberg in East Prussia. The trap extended from 0·17 to 5·42 m and was divided into seven sections with mean heights of 54·5 (1·8 ft), 129·5, 204·5, 279·5, 354·5, 429·5 and 504·5 cm (16·5 ft). There is nothing in the original paper to indicate the ground cover, except that the site was 80 m (250 ft) from building and trees, but values of 24 cm for $\overline{d}$ and 9 cm for Z_o were fitted and these suggest grassland with vegetation about 30 cm (1 ft) high. The catches are shown

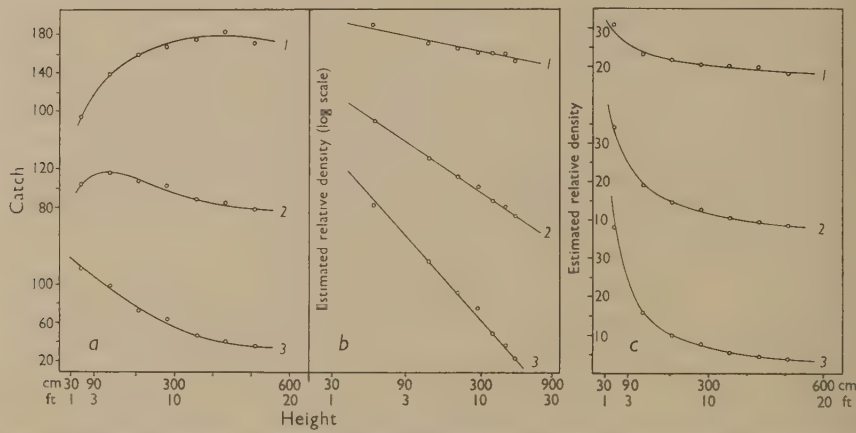


Fig. 2. Körting's (1931) data: *a*, Catch profiles; *b*, log density profiles; *c*, arithmetic density profiles. 1, thrips; 2, all insects; 3, frit-fly.

in Fig. 2*a* and the estimated density in Fig. 2 *b* and *c*. The wind profile used to convert the mean catch seems also to convert the separate groups equally well (the two species of thrips were not separated in the original paper).

(*b*) *Data of Profft* (*1939*)

A framework of two 2·75 m (9 ft) upright poles carrying six horizontal, adhesive-coated slats at mean heights of 17 (0·6 ft), 64, 115, 166, 217 and 268 cm (8·9 ft) was used by Profft to study aphid dispersal at Dramburg in east Pomerania. The traps faced north-west in a stubble field, and a photograph shows the harvested crop standing in stooks and another crop near by. The wind profile fitted has values of $\overline{d} = 20$; $Z_o = 24$ which indicates a low crop with very considerable irregularity. The lowest trap appears, from a photograph, to be below the level of vegetation, except where this is trampled down near the trap. The results for this lowest trap must therefore be treated with reserve, especially as coccinellids were collected in

August 1937 and psocopterons in September; only aphids were collected in both months and the wind profile possibly changed in a month. Only eighty-five coccinellids and sixty-three aphids were caught and the catch was uneven in time and space. However, they are all given in Fig. 3, because they are so frequently quoted.

(*c*) *Data of Shands, Simpson & Dudley (1956)*

The excellent aphid records of these authors obtained in different years and places with different kinds of traps are treated individually.

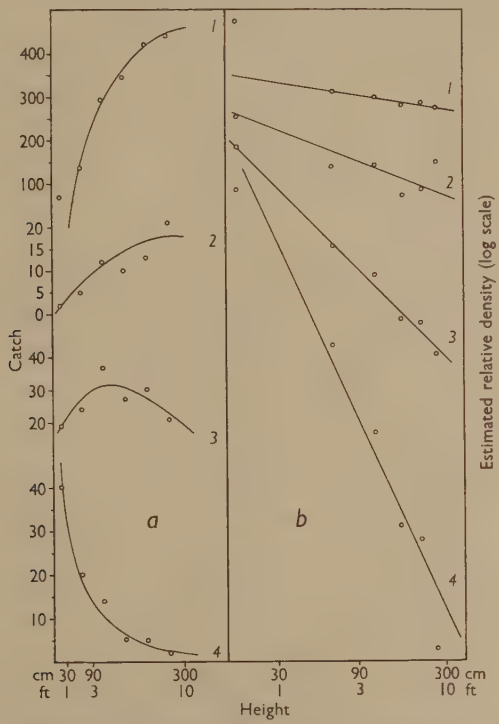


Fig. 3. Profft's (1939) data: *a*, catch profiles; *b*, log density profiles. 1, Psocoptera; 2, Aphidae; 3, all insects; 4, Coccinellidae.

Maine, U.S.A. 1942-44. The traps were basically nets with a 1 ft square inlet. A vertical series of traps was operated each year in the same place on Aroostook Farm near Presque Isle at 6, 11, 16, 21 and 26 ft (180 to 780 cm) from 16 August to 26 September 1942 and at 5, 10, 15, 20, 25 and 30 ft (150 to 900 cm) from 13 August to 18 September 1943 and 6 August to 14 September 1944. The traps were free to rotate into the wind and were pivoted on a rope stretched vertically between two crossbars connecting two upright poles. The nearest obstruction to wind was a

small orchard and two small buildings about 180 ft (56 m) to the east. The immediate neighbourhood was occupied largely by potatoes; the trap appears, from a photograph, to stand alongside a track next to a potato crop.

Three species of aphid were collected daily, the buckthorn aphid (*Aphis abbre-*

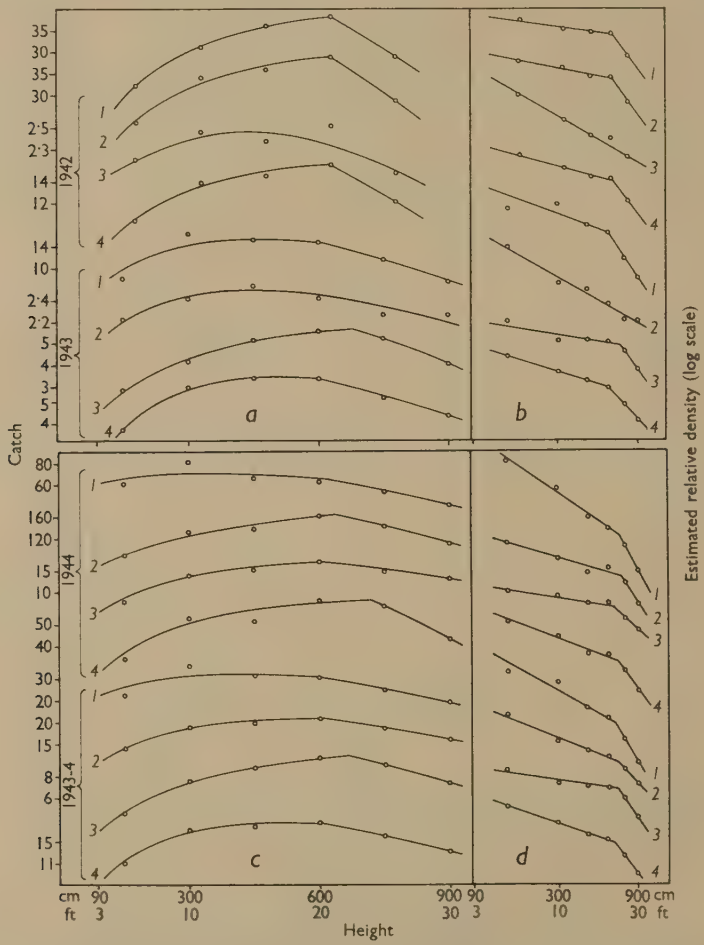


Fig. 4. Shands, Simpson & Dudley (1956), Maine data: *a* and *c*, catch profiles; *b* and *d*, log density profiles. 1, *Aphis abbreviata*; 2, *Myzus persicae*; 3, *Macrosiphum solanifolii*; 4, all aphids.

viata Patch), the green peach aphid (*Myzus persicae* Sulz.) and the potato aphid (*Macrosiphum solanifolii* Ashm.); a mean log daily catch is given in Table 2 of the original paper. From this table mean values were obtained and all the 1943 and 1944 catches were pooled to estimate the wind profile, as the trap site was constant; 1942 was omitted because the heights were different. This wind profile ($\bar{d} = 80$;

$Z_o = 20$) was applied to each species separately for 1943, 1944 and also for 1942. It was also applied to the grouped means for all species for 1942 (see Appendix A), 1943 and 1944, and to each separate species with the last two years taken together. The results are shown in Fig. 4 *b* and *d*; the catches are in Fig. 4 *a* and *c*. The conversion is equally effective for all species and years in any combination and this is particularly notable for 1942, which was not included in the data used to derive the wind profile. There is usually a change in gradient at about 20-25 ft.

So far the justification for fitting a specific wind profile is that it has been applied to catches (individual species) other than those from which it was obtained (the mean of all species or from different years). The remaining sets of data from Shands, Simpson & Dudley (1956) provide no further evidence upon this point, for only one species of aphid, the pea aphid (*Macrosiphum pisi* Harris), was collected.

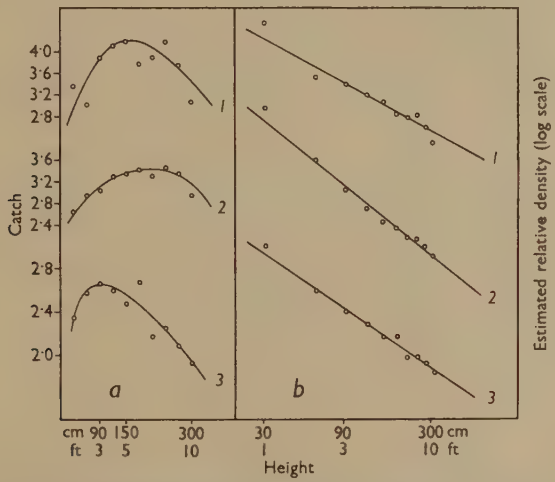


Fig. 5. Shands, Simpson & Dudley (1956), New York data for *Macrosiphum pisi*: *a*, catch profiles; *b*, log density profiles. 1, location 3; 2, location 1; 3, location 2.

NEW YORK, U.S.A. 1927. The traps used in this experiment were screens of 12 mesh wire gauze, 30 in. wide, coated with adhesive and stretched vertically from 6 in. to 10 ft 6 in. (15 to 315 cm). Three such traps were operated from 21 May to 22 August on farms near Geneva, N.Y. The traps were divided horizontally into 1 ft strips with means at heights of 1, 2, 3, 4, 5, 6, 7, 8, 9 and 10 ft (30 to 300 cm) and the catches recorded daily. Mean log daily catches are given in Table 4 of the original paper, and from these the geometric mean catches were obtained. They are given along with the estimated density profiles in Fig. 5. Values for $\bar{d}$ and Z_o respectively were 40 and 17·5 at location 1, 20 and 10 at location 2, 34 and 8 at location 3. The lowest foot or so of the trap must be at or below crop level and the wind speeds are read off from the tail of the profiles.

WISCONSIN, U.S.A. 1923-28. Sticky screens, similar to those at Geneva, were

used but the traps extended from 2 ft 6 in. (75 cm) upwards. Two screens were used each year in different but similar locations by fields of English peas 'with no near-by obstructions to wind movement'. The traps extended up to at least 29 ft 6 in. and the pea crop almost reached the bottom of the screen. The results are

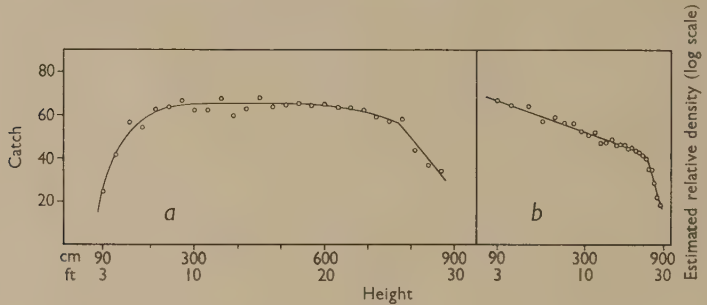


Fig. 6. Shands, Simpson & Dudley (1956), Wisconsin data for *Macrosiphum pisi*: *a*, catch profile; *b*, log density profile.

given as mean logs per trap per year in 1 ft intervals up to 29 ft (870 cm). The exact locations differed from year to year so that the fitted wind profile can only be approximate, but with large values for $\overline{d}$ (60) and Z_o (16) this is of less consequence than if the traps were set in a lower crop. The experiment lasted for 6 years with from 17 to 103 days trapping per year at one site and 7 to 64 days at the other. The catch and the density are shown in Fig. 6.

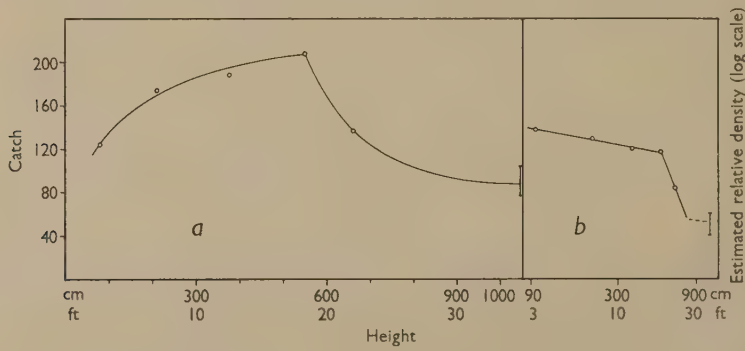


Fig. 7. Riggert's (1931) data for frit-fly: *a*, catch profile; *b*, log density profile.

(*d*) *Data of Riggert (1931)*

Riggert did three experiments, each lasting only 1 week. Only one covers a sufficient range of heights to be of value for this analysis. Again, only one species of insect was collected, *Oscinis frit* L., the frit-fly. From 16 to 23 July 1930 a mast was ringed with adhesive at five heights up to 6·7 m (22·3 ft) and in addition a flagpole about 40 m (133 ft) away was ringed at 10·7 m (35·7 ft). The exposed area

of the last trap is not recorded accurately (see Appendix B); the catch per unit area and the estimated density consequently cover a small possible range, as shown in Fig. 7. Values of 30 and 8 for Z_o and $\bar{d}$ were used and the result is interesting because of the change in gradient above 5 m, which compares with those aphid records extending to similar heights.

THE PROFILE OF INSECT DENSITY IN RELATION TO HEIGHT

(*a*) *The general nature of the profile and its importance*

Wherever or whenever two or more groups of these small insects were trapped simultaneously at several heights, a linear relationship between log density and log height is produced by the conversion suggested. As so many different types of curves, the catch profiles, convert to a series of straight lines differing only in gradient, the log density profiles, the conversion seems valid at least in principle if not in detail. It is perhaps even more convincing that, when traps were set up in the same position, the conversion from one year was equally effective when applied to another year (Shands, Maine data).

The gradients of the resulting density profiles are also reasonable, for they are similar for different species of aphids, even at different places—shallow for aphids, thrips and psocids; steeper for frit-fly and steepest for coccinellids. Hence, although the insects' mass, flight power and behaviour affect the gradient of the density profile, the continuously diminishing nature of the profile is common to all the species studied and so is mainly a property of the air movement. By the same reasoning it follows that the density profile need not be perfectly straight, although this was the most satisfactory form for demonstration; it need only be common to all groups converted by the same wind-speed profile, and could possibly be slightly curvilinear.

Whether curved or straight the diminishing density × height relation can be used to reconsider what has been concluded about the flight of small insects near ground level from studies with sticky traps. For example, Shands, Simpson & Dudley showed statistically significant differences between the height of the maximum catch of aphids of different species at different locations and at different times. They conclude that 'each species exhibited its own rather definite pattern of height distribution'. This is true, for in its context it is clear that it is catch that is referred to. However, using sticky traps at three heights and comparing catches of aphids, Broadbent (1948) wrote: 'It is obvious that during this period the four species (*Myzus persicae, Caveriella aegopodii, Metapolophium dirhodum*, and *Aphis fabae* complex) tended to fly at different levels.' Unfortunately, this can be interpreted as meaning that the aphids chose to fly at these levels whereas this choice has definite physical limitations imposed upon it. Later authors using sticky traps at a single height attempted to account for the differences between catches of different species of aphids by their different height distribution (*e.g.* Watson, Hull, Blencowe & Hamlyn 1951). The difference in height distribution of two species can be exactly paralleled by the height distribution of the same species in two

different places (see Fig. 5) when impaction-trap catches are used without conversion. This is because the curves produced by plotting the catch of impaction traps against height are a characteristic of the trapping situation rather than of the behaviour of the insect population.

In Fig. 8 a series of linear log × log density gradients, for some imaginary insect, are converted to impaction-trap catches in the wind-speed profile given in Fig. 1*d*, *i.e.* over spring wheat 60 cm high. All the typical catch profiles appear in this example as the density gradient changes, and all these gradients are possible with the same insect in different climatic conditions. The maximum in the catch profile

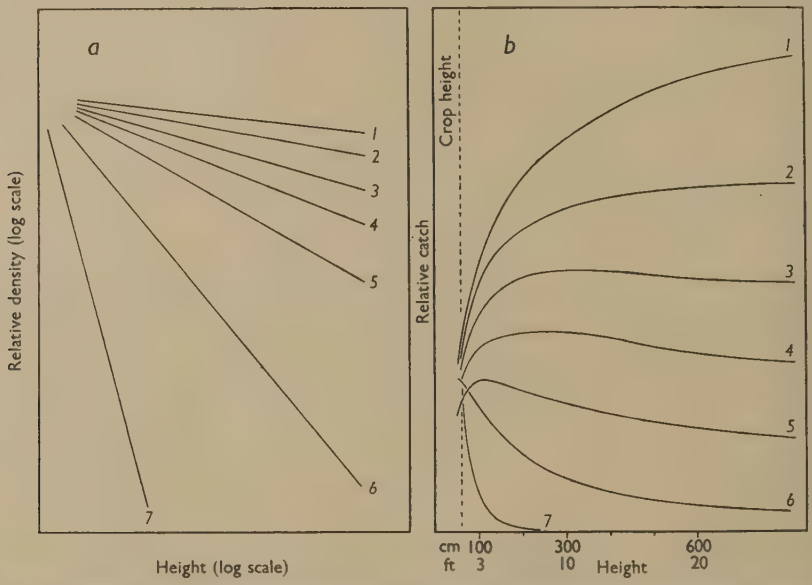


Fig. 8. *a*, a series of hypothetical linear log density profiles; *b*, catch profiles resulting from the density profiles shown in *a* when sampled by impaction traps in the wind profile over a 60 cm wheat crop (Fig. 1*d*).

moves progressively higher as the density profile becomes shallower. A very steep density profile produces a maximum so close to the ground that the catch curve appears hollow; at the other extreme a horizontal density profile gives a continuously rising catch profile following the wind profile. Between these extremes there will be a visible maximum in the catch profiles; its height will be a product of the interaction between the wind and density profiles. Even if the true density profiles are not linear on the double log scale, this effect will still occur to some extent with traps depending for their catch on the wind.

Most of the trapping was done, in the words of Shands, Simpson & Dudley, 'to indicate the importance of low-elevation movement of winged aphids (or other insects) as a means by which fields ... become infested ...'. It is therefore important to realize that, except for the isolated tree, which filters out the insects passing a

point, infestation of any fairly large expanse of vegetation is only possible by the insects at the base of the density profile, *i.e.* in the region of lowest wind speed, where flow is least but density is probably greatest.

The density profile, which is equally important in dispersal as it is in crop infestation, is maintained by the constant interchange of insects between all layers of the air; take-off and alighting are also part of the process (Johnson 1957b, Taylor 1958). The differential rate of horizontal movement at different heights in the wind, an integral part of the impaction trap catch, is otherwise of little importance, for insects are constantly passing from one wind-speed layer to another.

(*b*) *The precise form of the density profile*

If the log of the density is not strictly linearly related to the log of the height, there should be some trend of the points away from the fitted lines of Figs. 2 to 7, or the conversion to density must involve an additional element of correction that straightens the original curve. Careful examination of Fig. 2*b* shows that a very slight, downward curve might give a better fit to the five points at the highest levels for the mean of the two insects. There is no significant trend evident in the lines on Fig. 3*b*, except that for coccinellids which again bends downwards; nor in Fig. 4 *b* and *d*, except for the change in gradient about 20-25 ft. In Fig. 5*b* there is again a slight downward curve visible in the highest four points at locations 1 and 2. Fig. 6*b*, with a long series of closely fitting points, should show any trends, but the only one evident is again a slight curve, convex upwards, at the heights (19 to 24 ft) just below the change in gradient.

As pointed out earlier (p. 47) the values of $\bar{d}$ and Z_o used in the conversions are open to question. In the classical experiments on wind-speed profiles (see Sutton 1953) the values of Z_o do not exceed 10. Penman (in litt.) says that $\bar{d}+Z_o$ is less than crop height. Jensen (1954) gives evidence that for 'stipiform crops' Z_o approximates to 0·35 $\bar{d}$, and $\bar{d}$ is equal to mean crop height, although the maximum height of $\bar{d}$ measured was 30 cm. These values are for wide expanses of very regular surfaces. For example, Deacon (1949) suggested that his profiles for short grass might have been affected by the rough downland beyond the prepared site which was 200 yd square. Such uniform terrain is unlikely in the experiments analysed here, so that values of Z_o may be expected well outside the limits quoted above. Sutton (1953) points out that Z_o varies with temperature gradient and quotes Deacon (p. 240) as suggesting that $\bar{d}$ and Z_o be chosen independently to give the best fit, which can then be very accurate, at least over grassland.

It appears that although $\bar{d}$ or $(\bar{d}+Z_o)$ may be expected to be related to some extent to the plant height, and Z_o may be about 0·25 $\bar{d}$, these values are flexible, and irregularities in the ground cover, such as the edges of crops, may well affect the profile considerably. The wind-speed conversion is in fact empirical, and trial of many values shows that the sum of $\bar{d}$ and Z_o is the major factor; variation of either value within fairly wide limits has a relatively small effect beyond this. The values in Fig. 2*b* ($\bar{d} = 24$; $Z_o = 9$) are therefore considered very reasonable. Those in Fig. 3*b* ($\bar{d} = 20$; $Z_o = 24$) may appear improbable, but there were many

obstructions to free flow of air and it is impossible to decide. Those used for Fig. 5*b*, locations 1 and 2 (40 : 17·5 and 20 : 10) are inclined to be high for roughness coefficient. The values used in Fig. 5*b*, location 3 (34 : 8), Fig. 4 *b* and *c* (80 : 20), Fig. 6*b* (60 : 16) and Fig. 7*b* (30 : 8) are apparently almost ideal. The values of $\bar{d}$ and Z_o may be too high; they are almost certainly not too low. This conclusion is supported by the scatter diagrams, which suggest that the profiles should, if anything, be slightly convex upwards. The objection to a straight log × log profile, that it implies infinite density at zero height, is probably not important because the profile is usually intercepted by vegetation before it reaches ground level.

It is relevant to consider how these records compare with those at higher levels. Only the data of Glick, Freeman and Johnson can be converted to aerial density. They are plotted in Fig. 9 along with the curve for Shands's data from Maine, the most comprehensive of the low-level material, for although it deals only with aphids, it covers a long period at a single site. The high-level curves are for all insects, most of which are small. The curves for aphids alone are not appreciably different, but as they contain fewer individuals they are less reliable. The densities from Glick, Freeman and Johnson are absolute; that from Shands is relative and has been adjusted to end where Johnson's curve begins. The region between 20 and 50 ft appears to contain a discontinuity not covered by data at present available, but the general trend of the gradients shows a reasonable agreement.

Our more recent results using suction traps extend from 10 ft to 1000 ft (Johnson & Taylor 1955a) and link these two regions, but the intervals may be too large to investigate this particular problem fully, and intensive measurement over the first 100 ft is necessary. However, an example is given, using aphids caught on the morning and afternoon of 8 August 1955; there is some change in gradient between 20 and 50 ft for which meteorological factors alone are unlikely to be responsible.

THE BOUNDARY LAYER

The gradient changes at 20-25 ft in most records that extend above this level and this change is unlikely to be accounted for either by meteorological factors or a discontinuity in the wind profile. Only frit-fly and aphids are represented in these experiments. Below the level at which wind speed and the insect's flight speed are equal there is a boundary layer of relatively still air, within which height and direction of flight are apparently under full control of the insect. The depth of this layer differs for different kinds of insects and different occasions; for example, with aphids it is very shallow because they fly slowly (see p. 45), but in completely calm air it could become indefinitely deep, and is then limited only by the flight behaviour of the aphid. Migrant aphids tend to take off upwards, attracted by light, but at some level the light stimulus will no longer be unilateral as it is at take off. Light may, then, distribute aphids relatively uniformly from take-off up to this level, but not above it. For other insects a similar situation exists, although the flight power and behaviour factors governing the depth of the boundary layer will differ, and distribution within it may be less uniform. This

difference is emphasized by many observations of migrant butterflies flying at particular heights (*e.g.* Williams 1958) and by general experience of entomologists with relatively large and powerful insects that spend most of their lives in a much deeper boundary layer than do aphids.

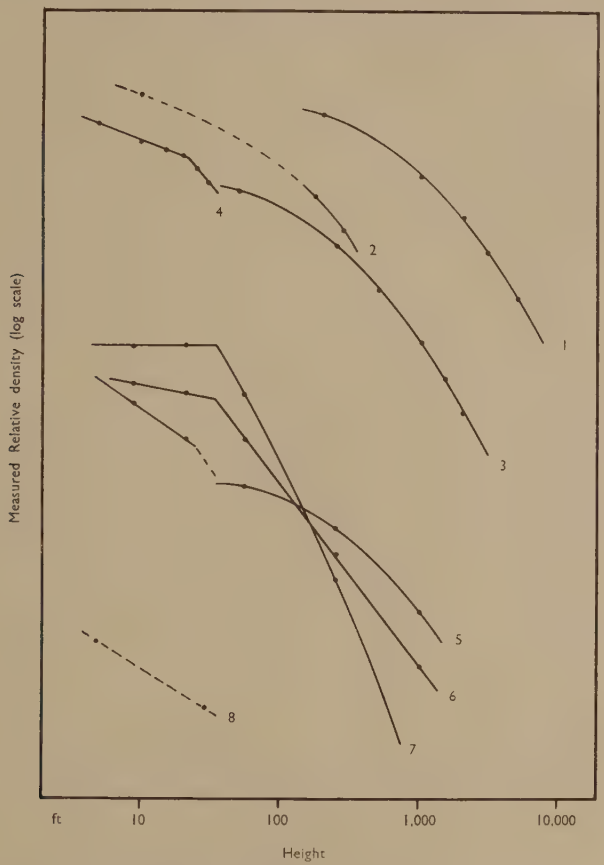


Fig. 9. Log × log density profiles: *1*, data of Glick (1939), all insects; *2*, data of Freeman (1945), all insects; *3*, data of Johnson (1957a), all insects; *4*, data of Shands, Simpson & Dudley (1956) from Maine, all aphids; *5*, suction-trap data 0900–1400 8 August 1955, all aphids; *6*, suction-trap data 0900–2000 8 August 1955, all aphids; *7*, suction-trap data 1400–2000 8 August 1955, all aphids; *8*, El Ziady's suction-trap data, all insects.

This shallow section of the gradient will be related to wind speed; in high winds it will be so small as to be difficult to detect, and will reach its maximum height in still air. It is therefore of interest to find that the data of Riggert (1931) on frit-fly, which show a similar change of gradient to aphids, were obtained during a week of mainly calm, dull weather. On the other hand Körting (1931) records

wind speeds of 1·5-3·8 m sec with a mean of 2·9 m/sec (13·9 m.p.h.) during his experiment, and his data show no boundary layer. The records of Shands, Simpson & Dudley cover such long periods that both kinds of situation usually exist. In these circumstances a second change of gradient, in the opposite direction to the first, may be expected somewhat higher. Such a stepped profile may be discernible in Riggert's results (Fig. 7*b*). A large and powerful insect that has a deep boundary

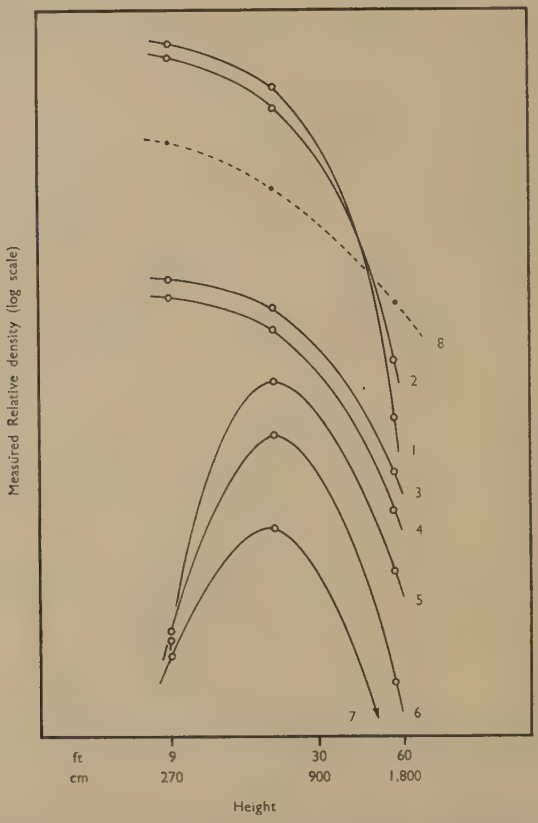


Fig. 10. Log × log density profiles for Macrolepidoptera and Heteroptera obtained by suction trap at Cardington, Bedfordshire: *Amphipyra tragopogonis*—*1*, 1954, *2*, 1955; other moths —*3*, 1954, *4*, 1955; *Agrochola lychnidis*—*5*, 1953, *6*, 1955, *7*, 1954; all heteroptera—*8*, 1953.

layer because of its higher flight speed, might more often be able to select a particular height for flight. This is particularly so with insects that fly at night when wind speed is usually less than during the day.

We have some records of 12 in. suction-trap catches at 9, 21, 56, 250 and 1000 ft (Johnson & Taylor 1955a). Suction traps measure insect density directly as they are relatively independent of wind for sampling efficiency (Taylor 1955). The

height distribution of the Macrolepidoptera, which are present in only the lowest three traps, can therefore be considered without the use of a wind profile. Fig. 10 shows the absolute density profile of the two commonest species, *Amphipyra tragopogonis* Clerck and *Agrochola lychnidis* Schiff, and the profiles for the other large moths lumped together. The catches are means for several weeks, the whole flight period for each species in each year when the traps were working (unpublished data). Although the profiles have only three points and the catches are few, the idea that some species select their height of flight when able to do so is strikingly confirmed. These moths have a wing span of about 1·5 in. and a probable flight speed (not measured) of about 15 ft/sec. It will be observed that, even if it were valid to do so, no amount of conversion by wind profiles could remove the maximum from these curves for *A. lychnidis*. Also the positions of the maximum in each of three separate years is strikingly constant, unlike the maxima for three species of aphid in different years (Fig. 4 *a* and *c*). Why *A. lychnidis* should choose to fly at 20 ft over an open expanse of grassland is not known. The curves for *Amphipyra tragopogonis* could also have a maximum between 9 ft and the ground which would not be detected, but for the remaining grouped species a continuously falling density seems more probable. This is also true for Heteroptera (data from Southwood 1959). However, most insects are less abundant at 30 ft than at 5 ft. El Ziady (1954) operated two 18 in. suction traps (Johnson & Taylor 1955b) at these levels in a sheltered garden for 2 years day and night, and the relatively few large insects were vastly outnumbered by the smaller ones. She concluded that, in general, the insect density at 5 ft was three times as great as the density at 30 ft, and although two points do not produce a profile, it is evident, when they are plotted (Fig. 9) alongside the other profiles, that the gradient is generally consistent with them.

ACKNOWLEDGMENTS

I would like to thank Mr M. J. R. Healy, Dr K. Mellanby and Dr H. L. Penman for their helpful criticism of this manuscript. I would also like to thank Dr Penman for the wind profiles in Fig. 1 *b*, *c* and *d*, and Dr G. W. Simpson and Mr W. A. Shands for being so helpful in seeking out old records.

SUMMARY

1. Various records of insects caught on sticky traps and in nets at several heights up to 30 ft were examined and the density distribution estimated in relation to height.

2. The insects concerned are all small: thrips, aphids, psocopterons, frit-fly and coccinellids. Their distribution appears to be consistent with that found for similar insects at greater heights.

3. Density diminishes regularly as height increases, except that gradients may change at 20-25 ft and between 30 and 50 ft.

4. It is suggested that these are the levels up to which such small insects fly in

still air, and that the predominance of winds above their flight speed is an overriding influence that produces the generally regular profile when all weather conditions are taken together.

5. This suggestion is partly confirmed by suction-trap catches which show a mean density for all insects three times as great at 5 as at 30 ft.

6. Larger insects such as moths behave differently; suction-trap catches show they can select a particular height of flight.

7. Catches on sticky traps were converted to densities by using a general wind-speed profile which, although open to some criticism, is not sufficiently in doubt to affect the main conclusions.

8. The curved distributions of insect numbers, which are often produced when sticky-trap catches are plotted against height and give maximum values at different heights on different occasions or for different species, are a product of the wind-speed and insect-density profiles, *i.e.* a function of the type of trap used rather than of the behaviour of the insect.

REFERENCES

Broadbent, L. (1948). Aphis migration and the efficiency of the trapping method. *Ann. Appl. Biol.* **35,** 379-94.

Davis, E. W., Landis, B. J. & Gibson, K. E. (1954). Aphid collections in the Yakima Valley of Washington, 1947-53. *J. Econ. Ent.* **47,** 1117-21.

Deacon, E. L. (1949). Vertical diffusion in the lowest layers of the atmosphere. *Quart. J. R. Met. Soc.* **75,** 89-103.

Dominick, C. B. (1943). Life history of the tobacco flea beetle. *Bull. Va. Agric. Exp. Sta.* No. 355.

El-Ziady, S. A. E. (1954). *Field Studies in flight activity of insects in relation to their physical environment.* (Ph.D. Thesis, London University.)

Freeman, J. A. (1945). Studies in the distribution of insects by aerial currents. The insect population of the air from ground level to 300 feet. *J. Anim. Ecol.* **14,** 128-54.

Gaines, J. C. & Ewing, K. P. (1938). The relation of wind currents, as indicated by balloon drifts, to cotton leaf-hopper dispersal. *J. Econ. Ent.* **31,** 674-7.

Glick, P. A. (1939). The distribution of insects, spiders and mites in the air. *Tech. Bull. U.S. Dep. Agric.* No. 673.

Goodwin, M. H. (1942). Studies on artificial resting places of *Anopheles quadrimaculatus* Say. *J. Nat. Malar. Soc.* **1,** 93-9.

Gregory, P. H. (1945). The dispersion of air-borne spores. *Trans. Brit. Mycol. Soc.* **28,** 26-72.

Hardy, A. C. & Milne, P. S. (1938). Studies in the distribution of insects by aerial currents. Experiments in aerial tow-netting from kites. *J. Anim. Ecol.* **7,** 199-229.

Jensen, M. (1954). *Shelter effect. Investigations into the aerodynamics of shelter and its effects on climate and crops.* Copenhagen.

Johnson, C. G. (1950). The comparison of suction trap, sticky trap and tow-net for the quantitative sampling of small airborne insects. *Ann. Appl. Biol.* **37,** 268-85.

Johnson, C. G. (1954). Aphid migration in relation to weather. *Biol. Rev.* **29,** 87-118.

Johnson, C. G. (1957a). The distribution of insects in the air and the empirical relation of density to height. *J. Anim. Ecol.* **26,** 479-94.

Johnson, C. G. (1957b). The vertical distribution of insects in the air and the temperature lapse rate. *Quart. J. R. Met. Soc.* **83,** 194-201.

Johnson, C. G. & Taylor, L. R. (1955a). The measurement of insect density in the air. Part II. *Lab. Pract.* **4,** 187-92.

Johnson, C. G. & Taylor, L. R. (1955b). The development of large suction traps for airborne insects. *Ann. Appl. Biol.* **43,** 51-62.

Körting, A. (1931). Beobachtungen über die Fluggewohnheiten der Fritfliege und einiger Getreidethysanopteren. *Z. Angew. Ent.* **18,** 154-60.

Lewis, T. (1959). A comparison of water traps, cylindrical sticky traps, and suction traps for sampling thysanopteran populations at different levels. *Ent. exp. & appl.* **2,** 204-15.

Nowak, W. (1951). Das Vorkommen der Grünen Pfirsichblattlaus (*Myzodes persicae* Sulzer) als Luftplankton in verschiedener Höhe über dem Erdboden. *Z. PflBau.* **2,** 123-30.
Prófft, J. (1939). Über Fluggewohnheiten der Blattläuse im Zusammenhang mit der Verbreitung von Kartoffelvirosen. *Arb. Physiol. Angew. Ent. Berl.* **6,** 119-45.
Riggert, E. (1931). Über die Flughöhe der Fritfliege. *NachrBl. dtsch. PflSchDienst, Berl.* **2,** 26-7.
Shands, W. A., Simpson, G. W. & Dudley, J. E. (1956). Low-elevation movement of some species of aphid. *J. Econ. Ent.* **49,** 771-6.
Southwood, T. R. E. (1960). The flight activity of Heteroptera. *Trans. R. Ent. Soc. Lond.* **112,**
Sutton, O. G. (1953). *Micrometeorology.* London.
Taylor, L. R. (1958). Aphid dispersal and diurnal periodicity. *Proc. Linn. Soc. Lond.* **169,** 67-73.
Taylor, L. R. (1955). The standardization of air flow in insect suction traps. *Ann. Appl. Biol.* **43,** 390-408.
Watson, M. A., Hull, R., Blencowe, J. W. & Hamlyn, B. M. G. (1951). The spread of beet yellows and beet mosaic viruses in the sugar-beet root crop. I. Field observations on the virus diseases of sugar-beet and their vectors *Myzus persicae* Sulz. and *Aphis fabae* Koch. *Ann. Appl. Biol.* **38,** 743-64.
Wolfenbarger, D. O. (1946). Dispersion of small organisms, distance dispersion rates of bacteria, spores, pollen and insects; incidence rates of diseases and injuries. *Amer. Midl. Nat.* **35,** 1-152.
Williams, C. B. (1958). *Insect migration.* London.

APPENDIX

A. Most of the original data used in this analysis are easily available and therefore have not been reproduced here. The paper by Riggert (1931) is, however, difficult to obtain. The appropriate table is therefore given below.

Trap heights and catches in Table 2 of Riggert (1931)

	Trap height (cm)	Exposed surface (cm^2)	Catch	Catch per 2220 cm^2
1	82-117	2220	124	124
2	194-229	2120	170	174
3	353-388	1910	162	188
4	535-570	1715	161	208
5	653-688	1610	99	136
6	1070	1610-2220*	76	76-105

* The exposed surface at 1070 cm is given as 'about the same as the other traps'.

B. During the course of the analysis it became apparent that there were misprints in Table 2 of the paper by Shands, Simpson & Dudley (1956). Dr Simpson and Mr Shands provided this corrected table. The changes in no way affect their original conclusions.

Mean log (n+1) *daily catch at Maine in* 1942

Trap height (ft)	*Aphis abbreviata*	*Myzus persicae*	*Macrosiphum solanifolii*
6	1·3456	1·3669	0·3421
11	1·4944	1·5310	0·3931
16	1·5577	1·5536	0·3754
21	1·5838	1·5872	0·4000
26	1·4669	1·4628	0·3156

THE HYDROLOGY AND PLANKTON OF THE RIVER SOKOTO

By M. J. HOLDEN

*West African Fisheries Research Institute Field Station, Birnin Kebbi, Sokoto Province, Nigeria**

AND

J. GREEN

Department of Zoology, Bedford College, University of London

(With 12 Figures in the Text)

During the course of work on fish populations in the River Sokoto and its surrounding flood plain it was decided to investigate the hydrology of the river and seasonal abundance of plankton because it was considered that a knowledge of these would permit a better understanding of the populations and life cycles of the fish. The field work on which this paper is based was carried out by one author (M. J. H.) who is responsible for the part of the paper dealing with the collection of data, the physical climate, hydrology and phytoplankton. The second author (J. G.)

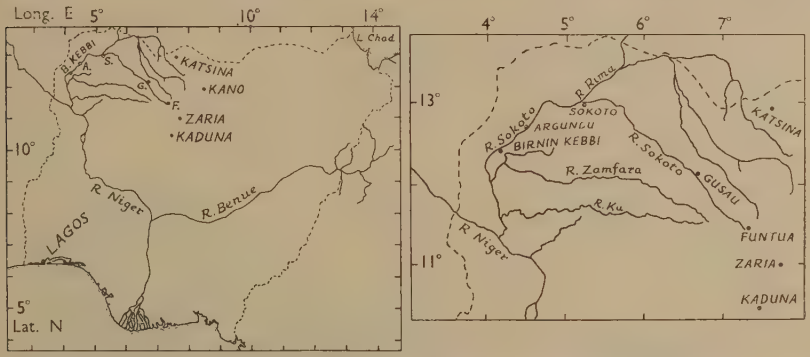


Fig. 1. Nigeria showing the Rivers Niger, Benue and Sokoto, and north-western Nigeria showing the River Sokoto system.

was responsible for working up the zooplankton collection and writing the part of the paper dealing with it.

THE AREA AND STATIONS

The River Sokoto is a tributary of the River Niger rising near Funtua in northern Nigeria (Fig. 1). From just upstream of the town of Sokoto the river bed is narrow with steep, rocky sides and is dry, except during the rainy season. To the west of Sokoto the river is joined by the River Rima and from there until it reaches the

* Present address: Fisheries Laboratory, Lowestoft.

River Niger there is permanent water, although the flow in the northern reaches may be slight at the end of the dry season. From Birnin Kebbi at least, and southwards, the river flows throughout the year, reaching a maximum rate of flow in the main channels of approximately 7 km h during the floods. From approximately the confluence of the Rivers Sokoto and Rima the banks flatten out and there is a large plain of varying width that is inundated when the river floods. A flood plain of this type is called 'fadama' by the Hausa natives. At Birnin Kebbi,

Fig. 2. Flood plain of the River Sokoto to the west of Birnin Kebbi with the two sampling stations shown.

where the present work was carried out, the flood plain is 8 km wide and bounded by an escarpment. At the height of the floods it is entirely covered with water and large areas are cultivated with deep water rice. As the river subsides to its dry season bed, which may be as narrow as 30 m, it leaves a series of pools that are permanent throughout the dry season. Fig. 2 shows that part of the flood plain to the west of Birnin Kebbi which is situated on the escarpment bordering the flood plain.

Two main stations were regularly sampled. One of these was a pool called Fesafari that became cut off during the dry season, and the other was in the main river (Fig. 2). Fesafari was 450 m long at the end of the dry season with a minimum recorded depth of 0·75 m on 5 April 1955 and a maximum depth of 4·5 m on 23 September 1954. The bottom was hard sand-mud mixture in 1954 but changed to soft mud, probably in the flood period of 1955. There was a fringing belt of water lilies that increased with the change over to a muddy bottom but the centre of the pool, where samples were taken, was always free of vegetation. It is linked to the river at the beginning of the wet season when the river reaches 0·7 m depth approximately. It is not possible to state a definite level because there is not a clear division between the pool and swamps that run into the river. The station in the river was selected because it was near an experimental set of gill nets and afforded a long reach in which to make zooplankton tows. The minimum depth was 2·5 m on 5 May 1954, and the maximum depth 7·5 m on 23 September 1954. There was a soft mud bottom and the area was free of vegetation. From time to time samples were taken at other points on the flood plain. These observations were not systematic and will only be referred to in discussion as required.

Sampling was first commenced at Fesafari and only later in the river. At first weekly observations were made, and pH, oxygen and temperature readings taken at the surface and 0·25 m from the bottom, or at 2 m intervals when the depth of the water was 4 m or more. These samples showed that there were little or no differences between depths and that weekly fluctuations were not marked. Thereafter sampling was done monthly as far as possible and at 1 m below the surface only unless the depth of water was less than 1·25 m, when it was done at 0·25 m from the bottom. No distinction has been made in the results between samples from different depths.

It was not possible to take samples always at the same hour and some of the fluctuations shown must be due to daily fluctuations in the values observed. River temperatures were recorded at three-hourly intervals on one occasion but it is possible that other values varied throughout the day; *e.g.* Blanc, Daget & d'Aubenton (1955) found that aquatic vegetation could cause a fluctuation of 2 pH units in 24 h. Therefore no account has been taken of minor fluctuations in considering the overall trends shown by the observations, the repetition in whose cycles from year to year confirms that the results are a true representation of hydrological and planktonic cycles in the river despite the imprecision of some of the data. It was not always possible to maintain the continuity of sampling. From May to October 1955 the writer was on leave. Accidents to equipment that could not be replaced quickly meant that sampling had to be discontinued, at least temporarily, or that observations could not be made as accurately as desired.

ENVIRONMENTAL CONDITIONS

(*a*) *Rainfall*

Rainfall figures were copied from those kept at the Government Hospital, Birnin Kebbi. Readings were taken at 0900 h each day to the nearest 0·01 in.

and have been converted to the nearest 0·1 cm. There is one wet season each year (see Fig. 3). The rains normally start in April but may not begin until May. There is no set pattern to the rains as can be seen by comparison of the histograms for the 3½ years. The earliest rains especially do not fall steadily but are torrential and are accompanied by violent thunderstorms. The heaviest rainfall occurring in any 24-hour period during the time of these observations was 11·4 cm. This caused a rise in river level of 0·18 m.

(*b*) *Air shade temperatures*

Those from February to November 1954 were read daily on a maximum and minimum thermometer by the Malaria Control Project personnel to the nearest degree F. Monthly means have been calculated and converted to the nearest 0·5° C below. From March 1956 to July 1957 daily temperatures were read at the Field Station on a maximum and minimum thermometer to the nearest 0·5° C.

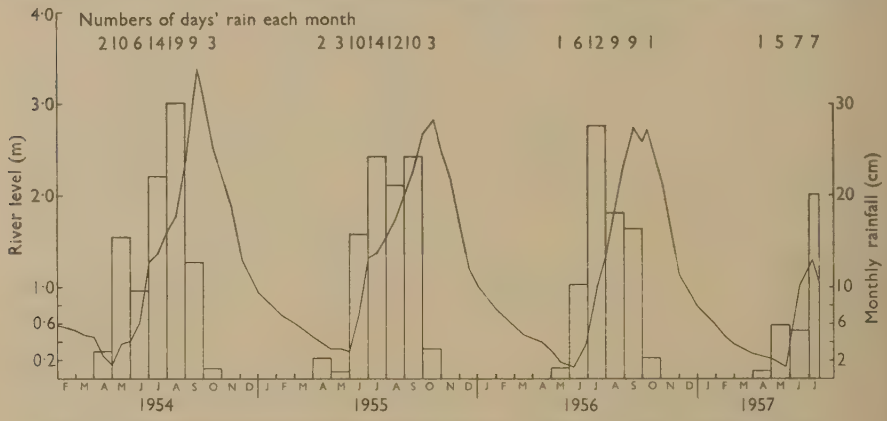

Numbers of days' rain each month
2 10 6 14 19 9 3
2 3 10 14 12 10 3
1 6 12 9 9 1
1 5 7 7
River level (m)
4·0
3·0
2·0
1·0
0·6
0·2
Monthly rainfall (cm)
30
20
10
6
2
J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J
1954
1955
1956
1957

Fig. 3. Monthly rainfall (histograms) and river level (continuous line) at Birnin Kebbi.

A Stevenson screen was not used at either recording point, a thatch cover being used. The results are given in Fig. 4. There is a hot season preceding the rains, which cause a rapid fall of temperature at their onset. With the cessation of the rains maximum temperatures start to rise until the beginning of the harmattan, a dry, dust-laden wind from the Sahara. Minimum temperatures fall rapidly, 9·5° C being the lowest recorded in January 1957. Maximum temperatures fall owing to the wind and dust obscuring the sun. The harmattan is followed by the hot season.

(*c*) *Water level*

Levels were measured on a depth gauge situated on the edge of the flood plain. Readings were taken to the nearest inch and converted to the nearest 0·01 m. For periods when the author was absent from Birnin Kebbi the records kept by the Native Authority were copied. The results are shown in the graph in Fig. 3. The

first rains do not affect the river level, which continues to fall, because they are absorbed by the parched soil or evaporated by the sun. The maximum height of the floods is not reached at the peak of the rains but later. This is due to rain in the

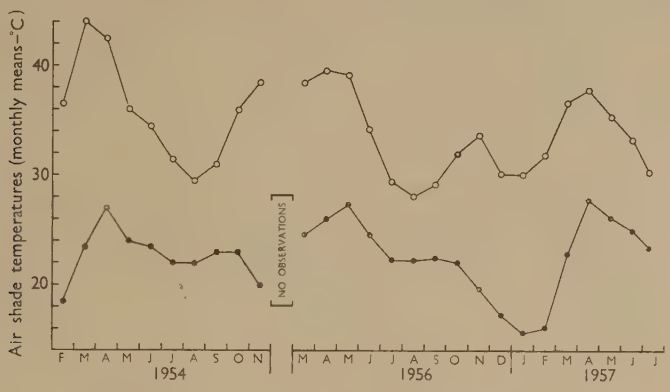


Fig. 4. Minimum and maximum air shade temperatures at Birnin Kebbi.

upper reaches of the River Sokoto near Funtua where the rains finish later than at Birnin Kebbi, and also to the flooding of the Niger which hinders the escape of water from the River Sokoto.

(*d*) *Water temperature*

Temperatures were read to the nearest 0·1° C holding the thermometer in a

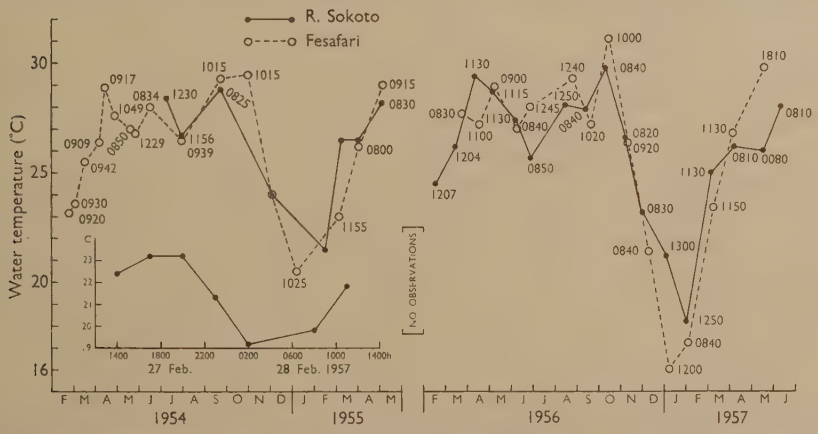


Fig. 5. Water temperatures in the River Sokoto and in Fesafari. Where available, the time of sampling is shown by each point. Inset shows daily fluctuation in river temperature for 27-28 February 1957.

bottle containing the water sample until a steady temperature was reached. The results are given in Fig. 5 with an inset showing the daily fluctuations over one 24-hour period, 27-28 February 1957. So that a comparison between the two

stations can be made the times of sampling have been given. In only one instance is there any large difference that is inexplicable on a time difference basis and that is in January 1957 and this was due to a rapid fall in air temperature between the two dates. The river was sampled on 3 January 1957 and the minimum air temperature for that day was 17·5° C and the maximum 31·0° C. Corresponding temperatures for 8 January 1957 when Fesafari was sampled were 10·5° C and 23·0° C. Most months did not show such large daily fluctuations in maximum and minimum air temperatures and the observed water temperatures are therefore a fairly true record of annual fluctuations.

For most months the water temperature follows the air minima. This is due to the fact that temperatures were taken usually before 1200 h, so that observations were nearer minimal rather than maximal temperatures. During the rainy season they approached maximal air temperatures although there was no difference in the times of taking temperatures. Macan (1958) explains this effect as being due to evaporation which reduces water temperature in dry weather.

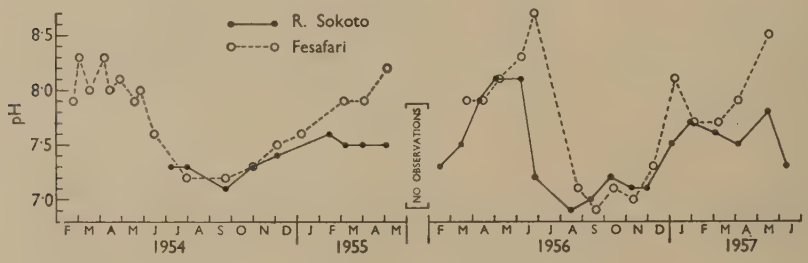


Fig. 6. Seasonal fluctuations in pH in the River Sokoto and Fesafari.

(*e*) *Hydrogen ion concentration and alkalinity*

During 1954 and 1955 a B.D.H. Capillator set was used in the field. During 1956 and 1957 a Lovibond Nessleriser was used and read in the laboratory. Comparisons showed that there was no change in pH during the time it took to transport samples back to the laboratory. Results are given in Fig. 6. The pH rarely fell below 7·0 owing to the calcareous soil through which the river flows at Sokoto. Alkaline waters are not typical of Africa. The high pH level at the end of the dry season is due to evaporation of the water and concentration of calcium salts (see Table 1). It rises higher in Fesafari because this is an isolated body of water, and this higher value is maintained longer until the pool is relinked with the river, when both values fall together owing to the influx of stagnant water of lower pH from the swampy areas and the dilution of calcium salts by rain water.

Alkalinity was measured with N/10 HCl prepared from B.D.H. standard solutions using methyl orange as an indicator. The results are given in Fig. 7 and agree with those for pH.

(f) Oxygen concentration

In 1954 this was determined by the standard Winkler titration. In 1956 and 1957 a Lovibond Nessleriser was used. The results are given in Fig. 7. The main factor affecting oxygen concentration appears to be wind. The rains are preceded by strong winds and the harmattan is accompanied by them and their wave action causes the May-June and January peaks. The concentration rises higher in Fesafari owing to its lesser depth. The low levels in July and August are due to the washing out of stagnant swamp water by the rains. The August-September peak is probably caused by an outburst of filamentous algae that occurred in all three years and was noted by its presence in the zooplankton samples and by its deposition on gill nets. The times of these observations are marked on Fig. 7. There is a delay between the first appearance of these algae and the rise in oxygen concentration due to a masking effect by the swamp water. Calculation of oxygen concentration as percentage saturation showed that temperature has very little effect on observed oxygen concentration.

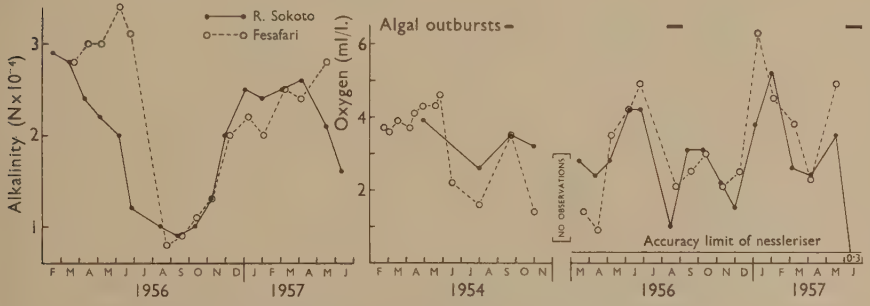


Fig. 7. Seasonal fluctuations in alkalinity and oxygen concentration in the River Sokoto and Fesafari. Outbursts of filamentous algae are indicated by horizontal bars.

(g) Transparency

This was measured with a 10 cm Secchi disc. The results are shown in Fig. 8. The main factor affecting water transparency is the zooplankton concentration which shows an incomplete inverse correlation with transparency. The transparency of Fesafari is for the most part greater than in the river although the zooplankton concentration is higher in the former. Fine silt held in suspension in the flowing waters of the river may be the cause of this.

The very high transparency of the water in October-November is due to the cessation of the rains when no further silt is being carried into the river off the land and before the plankton has started to increase. Daget (1957) found a similar increase in the Middle Niger.

(h) Chemical composition

Water analyses were done by the Government chemist, Kaduna. There was a delay of at least 48 hours between the time of collecting the samples and their

Table 1. *Chemical analyses (parts per million)*

	River Sokoto							Fesafari			
	13 Feb. 1956	2 Apr. 1956	4 June 1956	7 Aug. 1956	1 Oct. 1956	10 Dec. 1956	4 Feb. 1957	13 Feb. 1956	2 Apr. 1956	4 June 1956	4 Feb. 1957
NH_4	<0·004	0·004	0·004	0·102	0·05	0·12	0·012	0·093	0·14	0·299	0·012
Mg	7·0	10·0	9·0	2·0	3·5	4·0	9·0	7·0	10·0	9·0	7·0
Ca	32·0	42·0	32·0	12·0	10·0	28·0	32·0	28·0	30·0	32·0	28·0
Fe^{++}	0	0·2	<0·2	–	–	–	–	0	0·2	<0·2	–
Fe (total)	0·5	1·4	0·8	3·0	0·24	0·2	0·50	0·28	0·36	0·6	0·08
Mn	<0·025	0·075	<0·025	<0·025	<0·025	<0·025	<0·025	<0·025	0·025	<0·025	<0·025
Na	8·7	5·7	7·5	7·8	3·1	11·0	10·8	3·2	8·8	16·6	12·4
K	2·8	3·0	13·2	4·0	5·2	6·3	6·8	5·2	5·2	13·2	7·4
F	0·4	0·5	0·7	0·2	0·1	0·3	0·5	0·4	0·5	0·7	0·5
Cl	6·0	15·0	8·0	0·5	1·0	4·0	6·0	6·0	15·0	12·0	5·0
NO_2	0·046	0·07	0·007	0·01	<0·003	<0·003	0·003	0·231	0·03	0·03	<0·003
NO_3	0·44	0·132	<0·132	0·22	<0·11	<0·11	<0·025	<0·132	0·132	<0·132	<0·025
PO_4	<0·1	0·1	<0·1	<0·1	0·1	<0·1	<0·1	<0·1	0·1	<0·1	0·1
SO_4	0	tr	tr	0	0	0	tr	0	tr	tr	0
HCO_3	77·8	74·7	58·9	25·9	29·0	65·6	74·7	70·2	83·9	102·2	68·6
CO_3	0	0	0	0	0	0	0	0	0	0	0
SiO_2	20·0	16·0	10·0	10·0	14·0	12·0	11·0	16·0	12·0	12·0	14·0
Alkalinity, as $CaCO_3$	127·5	122·5	96·5	42·5	47·5	107·5	122·5	115·0	137·5	167·5	112·5
Hardness ($CaCO_3$)	75·0	85·0	95·0	27·5	34·0	79·0	103·0	60·0	70·0	95·0	85·0

tr, trace; –, no analysis.

arrival at Kaduna. The results must therefore be treated with caution because of possible bacterial and other changes, but the overall results agree with observations made at the Field Station. No separate samples were taken from Fesafari during the floods because other observations show that during this period there are no significant differences between the two stations.

The results are given in Table 1. The water is generally poor in nutrient salts. Sulphate is almost completely absent. This is typical of African inland waters (Beauchamp 1953). Phosphate is practically absent, while nitrate, nitrite and ammonia are all at low levels. Iron is present, the local soil having abundant laterite deposits. The rise in iron concentration in the rains is probably due to the

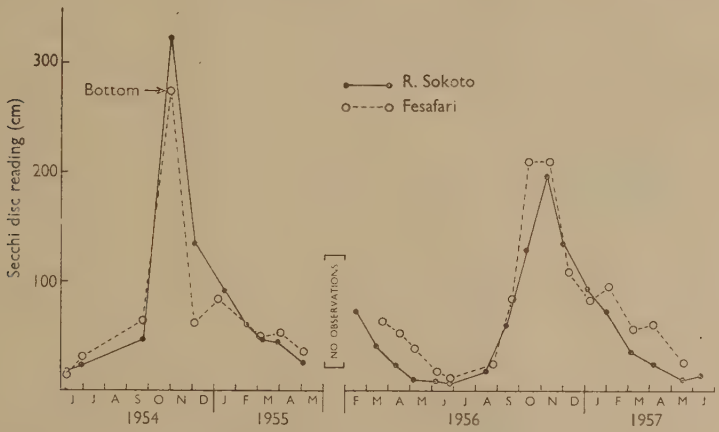


Fig. 8. Seasonal fluctuations in transparency measured with 10 cm Secchi disc in the River Sokoto and Fesafari.

release of iron at low oxygen tensions (Mortimer 1949). Calcium is abundant and total alkalinity correlates with pH observations.

(*j*) *Phytoplankton*

During 1954 and 1955 a few observations were made using a phytoplankton net. During 1956 and 1957 100 ml samples were filtered through a membrane filter using a Steffi-Cole's filter funnel and the phytoplankton preserved in 70% alcohol. The samples were examined by Dr E. Lind of Makerere College. It is difficult to draw conclusions from the results (Table 2) but it would appear that Fesafari has a higher productivity than the river, and that at both stations the productivity was greater in 1956 than in 1957. This can be partly associated with the concentration of nutrient salts. In February 1956 the concentrations of ammonia, nitrite and nitrate at both stations were higher than those in February 1957, and they were higher in Fesafari than in the river. This association does not extend into 1957 when there was little or no difference between the concentrations of these ions at the two stations despite the higher productivity in Fesafari. The low phyto-

plankton concentrations during the floods are due to the diluting effect of the rains both on the phytoplankton itself and on nutrient salts.

Records of a fairly superficial examination of phytoplankton samples from Fesafari on 6 January 1954, 6 January 1955 and 1 April 1955 and from the river on 1 April 1955 indicate that the same pattern of production is followed each year. The observation of 'Nothing' on 7 June 1956 suggests rapid fluctuations in the phytoplankton. There is a similar observation on 12 September 1956 whereas on 3 September 1956 filamentous algae had been recorded as abundant on gill nets. In 1954 this outburst occurred in the river and Fesafari at the same time, so that

Table 2. *Phytoplankton analyses*

	RIVER SOKOTO
16 Feb. 1956	Diatoms, *Cosmarium* occ.
6 Jun. 1956	Scattered cells of Myxophyceae
12 Sep. 1956	Nothing
7 Nov. 1956	Nothing
1 Dec. 1956	Nothing
3 Jan. 1957	Nothing
1 Feb. 1957	Nothing
4 Mar. 1957	Scattered cells of Myxophyceae
6 Apr. 1957	Scattered cells of Myxophyceae
	FESAFARI
23 Mar. 1956	*Synedra* c., *Melosira* occ., *Pediastrum* occ.
10 Apr. 1956	*Aphanocapsa, Merismopedia,* diatoms, *Pediastrum, Scenedesmus, Oscillatoria* fragments, all frequent
7 May 1956	*Aphanocapsa, Chroococcus, Melosira* (not common)
7 Jun. 1956	Nothing
25 Jun. 1956	*Melosira* and other diatoms, *Euglena, Phacus, Trachelomonas, Scenedesmus*
24 Aug. 1956	Nothing
19 Sep. 1956	Nothing
13 Oct. 1956	Nothing
10 Nov. 1956	Nothing
8 Jan. 1957	Nothing
3 Feb. 1957	Nothing
7 Mar. 1957	Occ. diatoms and *Euglena*
5 Apr. 1957	*Melosira, Euglena,* diatoms, *Aphanocapsa, Dictyosphaerium,* all occ.
17 May 1957	*Melosira, Euglena, Coelastrum, Oscillatoria,* all occ.

c. = common
occ. = occasional

their presence would have been expected in the samples of 24 August 1956 and 19 September 1956 both of which record 'Nothing'. While the coincidence of the samples from year to year and their similarity to the zooplankton results indicate that the picture of phytoplankton production is probably correct, the results cannot be considered a very detailed picture of this production.

ZOOPLANKTON

Timed tows were made using a net of 5 meshes per mm with mouth 30·5 cm diameter over an approximately fixed distance of 300 m. It was not always possible to make the tow over the same distance owing to obstructions such as long lines in

the water, nor at the same speed because high winds blew the boat along rapidly, but as far as possible tows were made comparable. They were made with the net just below the surface of the water; no meter was used. In Fesafari the tow was made from the north-east end of the pool in a westerly direction down the middle line into the southerly arm. In the river the tow was made from the westerly end of the reach marked (Fig. 2) upstream in a south-easterly direction.

(*a*) *Method of counting*

The sample in each tube was made up to 30 ml with 5% formalin, and the whole sample was thoroughly mixed. A sub-sample of 0·5 ml was quickly taken with a wide-mouthed graduated pipette and ejected into a petri dish containing a thin film of water. The water in the petri dish was agitated so that the animals were evenly distributed. The base of the petri dish had lines ruled with a diamond at intervals just a little under the field diameter of a binocular microscope with a magnification of 30 diameters, to aid in systematic searching and counting. All the animals in the sub-sample were counted.

The volume of animal material in each sample was estimated by allowing the sample to settle for 5 days and then measuring the height of material in the tube to the nearest millimetre. All the tubes were of the same diameter so that the volume of settled material could easily be calculated. When the sub-sample was taken for the count, an estimate was made of the amount of detritus and plant material in the sample. This was estimated after examination of at least ten fields of the microscope. The estimate was subjective, and attempted to assess the amount of non-animal material to the nearest tenth by volume, but because of the subjective method no claim to accuracy greater than one-fifth by volume is made. The estimate of non-animal material was always made before the count to avoid any bias due to previous knowledge of the number of animals in the sample. The estimated percentage of detritus was deducted from the volume of material in the tube to give an estimate of the volume of zooplankton.

In the results which follow counts have been presented in terms of major groups, and not divided into species. The systematics of some of the species are complicated and since they are not relevant to the purpose of the present paper they have been left for more detailed treatment elsewhere.

(*b*) *Rhizopoda*

The most striking feature of the seasonal occurrence of the rhizopods in the Sokoto is that they appear most abundantly at the times when other groups are relatively sparse. They are generally more abundant in the river than in Fesafari. According to Kofoid (1908) the appearance of testaceous rhizopods in river plankton can be due to two different causes. The first of these is the action of the river as it rises and flushes out rhizopods from swampy, heavily vegetated areas. The second cause is the production of light-shelled planktonic forms by species which are not normally planktonic. In the Sokoto the level of the river appears to be of overriding importance. Fig. 9 shows that in the river the abundance of rhizopods

in the plankton is greatest when the river is rising to its maximum height, and the lowest numbers occur when the river is very low. The relatively high numbers in the plankton of the river in March and April of 1956 may be due to the production of plankton forms by non-planktonic species; this question will be examined in more detail when the systematics of the Sokoto species have been worked out. When the relative importance of the rhizopods in relation to the rest of the zooplankton is considered there is a very good agreement with river level, as can be seen from the two lines in Fig. 9, where the rhizopods are plotted as a percentage of the total zooplankton. From September to December rhizopods formed between 40 and 50% of all the zooplankters.

Most of the species in the Sokoto belong to the genera *Arcella* (*A. vulgaris* Ehrenberg, *A. macrostoma* Penard, *A. dentata* Ehrenberg) and *Difflugia* (*D. corona* Wallich, *D. scalpellum* Penard, *D. acuminata* Ehrenberg, *D. limnetica* Levander). These species form the greater part of the rhizopods in all the samples, but various

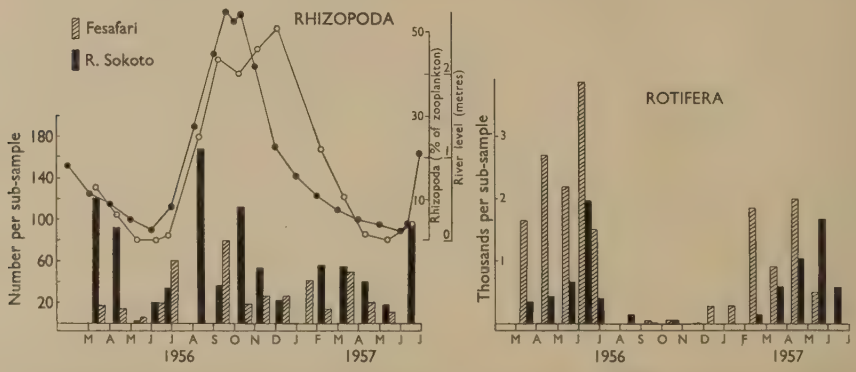


Fig. 9. Seasonal variation in abundance of Rhizopoda and Rotifera in the River Sokoto and Fesafari. Histograms give numbers per sub-sample. —o—o—, Rhizopoda as a percentage of the total zooplankton. —•—•—, height of the river.

other species are also found, such as *Centropyxis aculeata* Stein, *Euglypha acanthophora* (Ehrenberg) and *Lesquereusia spiralis* (Ehrenberg).

(*c*) *Rotifera*

The seasonal fluctuations in total rotifers are shown in Fig. 9. In both 1956 and 1957 the maximum production of rotifers was earlier and greater in Fesafari than in the river. The numbers in Fesafari in 1957 did not reach the same height as in 1956, but the numbers in the river did not differ significantly in the two years. The population peaks are produced by the following four species: *Brachionus caudatus* Barrois & Daday, *B. falcatus* Zacharias, *Keratella tropica* (Apstein), and *Tetramastix opoliensis* Zacharias. Of these the first is generally the most numerous, and *Brachionus falcatus* is more important in Fesafari than in the river. *Asplanchna brightwelli* Gosse forms up to 17% of the rotifer population in the river in April.

When the river is in flood the importance of these species is greatly reduced, and numerous other species appear, though the total number of rotifers is very much lower than in the dry season. The species appearing with the floods are dominated by several species of *Lecane*, including the following: *L. bulla* (Gosse), *L. ungulata* (Gosse), *L. leontina* (Turner) and *L. curvicornis* (Murray). Other species which occur frequently at this time include *Trichocerca bicristata* (Gosse) and *Macrochaetus collinsi* (Gosse).

(*d*) *Cladocera*

The dominant species in this group are *Diaphanosoma excisum* Sars, *Moina dubia* Guerne & Richard, and *Ceriodaphnia cornuta* Sars. These species are responsible for the population peaks shown in Fig. 10. In the River Sokoto the cladoceran population built up to high peaks in June in both 1956 and 1957, while in Fesafari 1956 produced a high peak, but the population failed to develop in 1957. In the period from August to March, when Cladocera are scarce, there is a change in the species which are present. The species listed above as responsible for the population peaks are rare or absent, while various others, which generally live on or near the bottom, are found. *Grimaldina brazzai* Richard, *Macrothrix triserialis* Daday, *Leydigia ciliata* Gauthier, *Alona verrucosa* Sars and *Chydorus barroisi* (Richard) have been recorded. Even the mud dwelling *Iliocryptus spinifer* Herrick appeared in some of the samples. The occurrence of such bottom-dwelling species in the plankton is associated with the swollen state of the river; the increased flow swirls such creatures up from the bottom into the plankton.

(*e*) *Copepoda*

The fluctuations in numbers of copepods throughout the year are shown in Fig. 10. The Calanoida were most abundant in Fesafari in June 1956, when the pool had five times as many as the river. In 1957 the calanoid population remained sparse, and the numbers in the river were a little higher than in Fesafari. Calanoids disappear completely from the samples during the period from August to November in Fesafari and for even longer in the river, where they are not found again until April. The Cyclopoida contrast with the Calanoida in being more abundant in the river than in Fesafari in June 1956. This group of copepods persists throughout the floods, but in greatly reduced numbers. The maximum numbers in both the river and the pool were lower in 1957 than in 1956. A few copepodid stages of a lernaeid were found in the samples (Table 3). The adults of this family are parasitic on the gills of fish, but the larvae are actively swimming members of the plankton, and seek out new hosts. The number of copepodid stages found was too small to enable any conclusions to be drawn about seasonal occurrence.

All copepod nauplii were counted together. They were found to persist throughout the year in Fesafari, though the numbers were very low during the floods. In the samples from the river no nauplii were found between the August sample and the December sample. The time of maximum abundance of nauplii coincides

with the maximum of the later stages. This is in agreement with the findings of Kofoid (1908) in the River Illinois, but disagrees in some respects with the work of Cohn (1903) who found that the maxima of nauplii preceded the maxima of later stages in two cases out of three in certain German lakes. Steur (1901), working on the Danube, found the maxima of nauplii coinciding with those of later stages on two occasions out of three. There is no real conflict in such results because an abundance of nauplii may be due to two causes. The first is a large hatch from resting eggs which may have been laid in the previous year. Nauplii may then be abundant without any adults being present. An example of this type has been described by Comita (1956) who studied a population of *Limnocalanus johanseni* in an Arctic lake. The second source of abundant nauplii is from eggs hatching from the sacs of mature females; in this case one would expect nauplii to be most

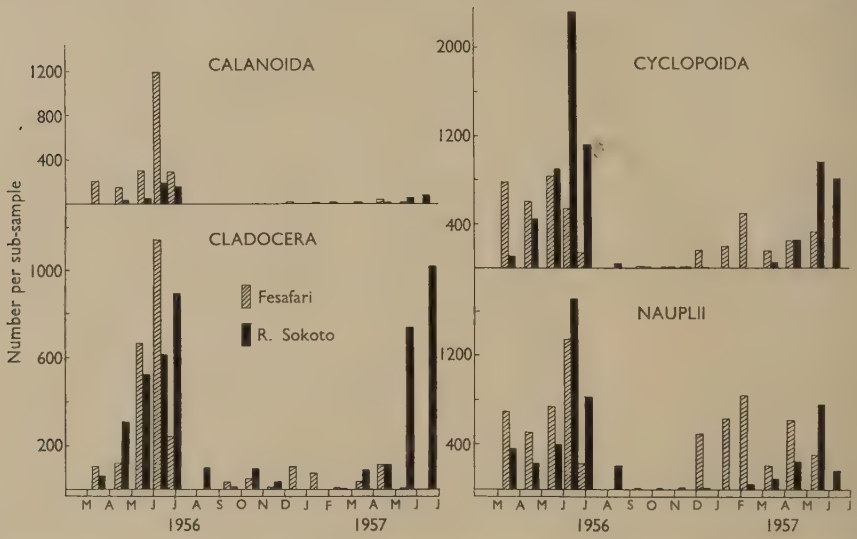


Fig. 10. Seasonal variation in abundance of Cladocera and Copepoda in the River Sokoto and Fesafari.

abundant when the adult population was most abundant. This is the situation found in the Sokoto.

(*f*) *Ostracoda*

The freshwater ostracods are mainly bottom dwellers, and their appearance in the zooplankton is adventitious. They are commonest in the Sokoto, as one would expect, when the river is in flood (Table 3).

(*g*) *Other groups*

The only truly planktonic species included under this heading is the freshwater medusa *Limnocnida tanganyikae* which appeared in Fesafari in January, February, March and April 1957.

The rhabdocoele turbellarians are mainly benthic in habit, but their occurrence

in the Sokoto does not show any marked correspondence with the floods. Some species are known to swim fairly well, and Kofoid records one occasion when 19 250 per cubic metre were found in the River Illinois. No such outbreaks were found in the Sokoto (Table 3).

Table 3. *Numbers of zooplankters in sub-samples from net hauls*

	Rhizopoda	Rhabdocoela	Rotifera	Cladocera	Cyclopoida	Calanoida	Nauplii	*Lernaea* sp.	Ostracoda	Insect larvae	Hydracarina
R. Sokoto											
1956											
14 Mar.	121	–	335	62	103	–	360	–	1	–	1
10 Apr.	93	1	438	310	441	25	234	–	–	1	3
5 May	3	–	659	521	897	54	392	–	1	1	–
6 June	19	–	1982	608	2316	191	1714	–	–	–	1
26 June	34	–	417	886	1111	145	830	1	1	–	–
14 Aug.	168	–	159	96	40	–	201	–	4	2	5
12 Sept.	36	2	22	10	6	–	–	–	1	2	3
9 Oct.	112	–	56	87	15	–	–	–	10	–	3
7 Nov.	53	–	19	34	5	–	–	–	–	1	3
1 Dec.	21	–	4	–	8	–	6	–	–	1	1
1957											
1 Feb.	56	–	140	5	9	–	41	–	–	1	–
4 Mar.	54	–	578	86	52	–	99	–	1	–	–
6 Apr.	40	–	1050	112	243	1	255	–	–	–	–
16 May	18	1	1695	737	965	43	768	2	–	–	1
10 June	98	2	580	1013	825	84	171	1	–	2	3
Fesafari											
1956											
23 Mar.	15	–	1649	104	781	198	702	–	–	–	–
18 Apr.	14	–	2692	719	599	142	517	–	–	1	–
7 May	6	–	2212	663	829	298	743	–	–	–	2
7 June	20	–	3890	1130	538	1190	1354	–	–	–	2
25 June	61	–	1507	273	127	285	299	1	2	–	–
19 Sept.	80	–	42	31	6	–	1	–	–	3	3
13 Oct.	18	3	50	46	4	–	1	1	2	2	4
10 Nov.	26	–	4	11	3	–	4	1	–	–	1
8 Dec.	25	1	276	99	164	9	476	–	–	–	2
1957											
8 Jan.	42	–	277	72	187	4	643	1	–	–	–
3 Feb.*	14	–	1838	11	494	8	856	–	–	1	1
7 Mar.†	50	1	889	33	149	4	216	–	–	1	–
5 Apr.	21	1	1996	112	238	30	635	1	–	–	1
17 May	11	–	486	4	323	2	312	–	–	–	–

* Also 2 *Limnocnida* medusae. † Also 1 *Limnocnida* medusa.

Insect larvae and Hydracarina occur sporadically in the samples throughout the year, but are most abundant during the floods.

(*h*) *Relative importance of zooplankton groups*

The figures showing seasonal distribution indicate that all the plankton groups except the rhizopods are most abundant in May and June, and it can be seen in Table 3 how the numbers of each group compare with each other. Another feature of importance is the composition of the plankton throughout the year; this is

shown in Fig. 11, where each group is plotted as a percentage of the total. It is evident from these figures that there are two distinct seasonal plankton assemblages. From January to July the Copepoda and Rotifera form the greater part of the assemblage, while from July to December the Rhizopoda increase in importance. The Cladocera also show a relative increase in importance, centred about October. We have already shown that there is a change in the cladoceran species present during the floods, and that the species present at this time are mainly bottom-dwelling species which as a rule are much smaller than true planktonic Cladocera. This means that in spite of an increased relative numerical importance the decrease in Cladocera at the end of June is even more marked, in terms of food material available for fish, than is shown in the histograms.

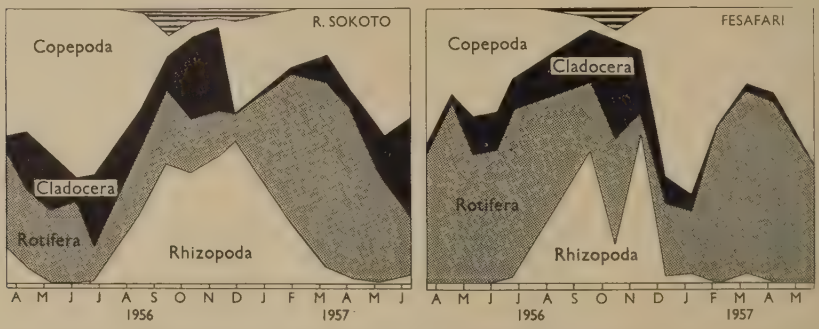


Fig. 11. Seasonal variation in the composition of the zooplankton of the River Sokoto and Fesafari. Each group is plotted as a percentage of the total zooplankton.

The occurrence and relative importance of non-planktonic groups in the samples coincide with the period of flooding. The duration of occurrence of these forms is longer in the river than in Fesafari, due no doubt to an earlier reduction in the rate of flow through Fesafari as the floods decline.

(*j*) *Total zooplankton*

Consideration of the total zooplankton has been left until the end so that the seasonal fluctuation of the whole can be viewed against the background of the fluctuations of the constituent groups. Seasonal fluctuations are shown in Fig. 12. The most obvious and striking feature is the great drop in both number and volume with the onset of the floods. The increase in zooplankton begins much earlier in the pool than in the river so that in the early part of the year, from January to May, there is about twice as much zooplankton in the pool as in the river. In both the pool and the river there was a much greater production of zooplankton in 1956 than in 1957. The reduction in production in the latter year was more severe in Fesafari than in the river, and the failure to develop can be attributed in particular to the Cladocera and Calanoida. It is noteworthy that both these groups feed mainly on small planktonic algae, while the Cyclopoida have a much greater range of diet (Fryer 1957). The amount of phytoplankton in Fesafari in 1957 was

noticeably smaller than in 1956, and this may be attributed to the lower concentrations of ammonia, nitrates and nitrites. In the river the reduction in numbers in 1957 cannot be attributed to the failure of the Cladocera; they were just as abundant as in 1956. There is also only an insignificant reduction in the Rotifera in the river. The copepod population is mainly responsible for the lower figures in the river in 1957. It is difficult to find any reason why this group, and particularly the Cyclopoida, should fail when the Cladocera increased to the level of the previous year.

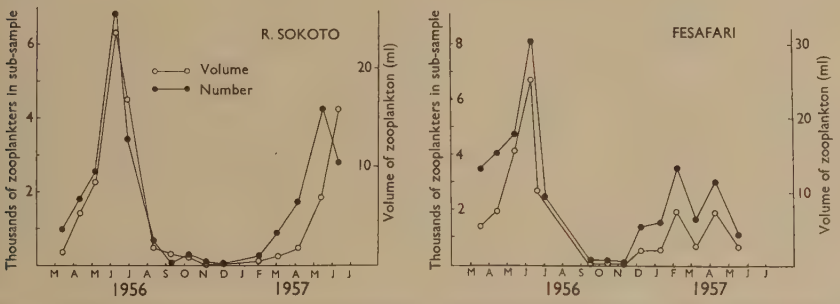

R. SOKOTO
Volume
Number
Thousands of zooplankters in sub-sample
Volume of zooplankton (ml)
M A M J J A S O N D J F M A M J J
1956
1957
FESAFARI
Thousands of zooplankters in sub-sample
Volume of zooplankton (ml)
M A M J J A S O N D J F M A M J J
1956
1957

Fig. 12. Seasonal variation in volume and numbers of zooplankton in the River Sokoto and Fesafari.

The two methods of estimating total zooplankton agree very closely. On only one occasion did the total number in the sample fall while the volume of the sample continued to rise. This was in the river from May to June 1957. The explanation for this is seen when the frequency histograms for the various groups are examined. The rotifers and nauplii decrease markedly at this time, while the Cladocera increase. Each cladoceran is as large as 200 rotifers, so that a small increase in Cladocera could more than compensate, in terms of volume, for a considerable reduction in the rotifer population.

Table 4. *Maximum numbers recorded per m³*

	Cladocera	Copepoda	Rotifera
River Sokoto	2700	7500	6000
Fesafari	3400	5100	11 700
Blue Nile (Rzóska *et al.* 1955)	108 000 (all Crustacea together)		202 000
Illinois (Kofoid 1908)	440 000	1 000 000	5 000 000

In the main part of this paper no attempt has been made to express the abundance of the various zooplankters in absolute quantitative terms. The sampling method was too crude to allow this. A rough calculation can, however, be made to get an idea of plankton production in the Sokoto to compare with other localities. In this calculation there have been no corrections for the net filtering rate, or for variation in the time taken to complete a tow, which varied somewhat with the prevailing wind. We have calculated that each sub-sample represents about $\frac{1}{3}$ m³ of water. When the figures for rotifers, Cladocera and copepods are converted

to numbers per cubic metre they can be compared with the figures published by Kofoid (1908) for the River Illinois and those of Rzóska, Brook & Prowse (1955) for the Nile. In Table 4 maximum figures are given since these probably provide as good a basis for comparison of production as any other. The table shows that the temperate, polluted Illinois is very much more productive than either the Nile or the Sokoto. Even allowing for the crudity of sampling of the Sokoto there can be no doubting the paucity of production in this river. It is relevant to note that the values for nitrate from waters of the Illinois are sometimes ten or twenty times as high as those recorded from the Sokoto.

DISCUSSION

The hydrology and plankton of the River Sokoto are dominated by the water level. During the flood period the volume of water entering the river is so great that it dilutes the plankton and important chemical contents to a considerable degree so that the plankton crop, while possibly as large overall as in the dry season, is small per unit volume of water. The great dilution of nutrient substances inhibits the development of the phytoplankton. It is only when the rains cease that the level of nutrient salts can start to rise, and even at the end of the dry season this leaves certain ions limiting. Probably the chief limiting ion is sulphate. The amount of this ion in the water of the Sokoto is extremely small, and there is some indication from the work of Fish (1956a) and Beauchamp (1953) that sulphate acts as a limiting ion in other African waters. Phosphates are also scarce in the Sokoto, but Komarovsky (1953) found that minute traces were sufficient for diatom production, although it was increased by their addition. In Fesafari, where concentration due to evaporation starts earlier and can go on longer there is a greater plankton production than in the river, but, as the zooplankton figures in Table 4 show, production is very poor compared with other similar waters.

While the concentration of nutrient salts is generally low, there is a high calcium concentration in the river due to its flowing through calcareous soil at Sokoto. Daget (1957) gives a calcium concentration of 3 mg/l. for the River Niger at Diafarabé; this is well below the lowest concentration (10 mg/l) found in the Sokoto. The alkalinity in the Sokoto is also high, the highest value being 0·0034 N, compared with 0·00115 N recorded by Daget in the Middle Niger. The alkalinity of the Niger is usually much lower than this maximum figure; Daget gives a figure of 0·0004 N, while a similar figure of 0·0006 N is given by Johnels (1954) for the River Gambia. Only at the beginning of the rains was a comparable figure observed in the Sokoto. The alkalinity of the Sokoto is correlated with a high pH, which rarely fell below 7. Blanc, Daget & d'Aubenton (1955) obtained pH values of 6 to 7 in the River Niger, but observed rapid fluctuations which would be expected with a low alkalinity. Johnels (1954) found the pH varying between 7·0 and 7·5 in the River Gambia, but in the associated swamps it fell to 4·3.

Temperature appears to be of little importance in the nutrient and plankton cycles in the Sokoto, but the low values in December and January probably delay the plankton outburst by slowing down rates of growth and reproduction.

The oxygen concentration had no observed effect, although the work of Fish (1956b) shows that the level to which the oxygen concentration falls at the beginning of the rains is below the 100% saturation level of the blood of *Lates albertianus* Worthington and *Tilapia esculenta* Graham. The Sokoto species of these two genera might be expected to have similar blood-loading capacities. The local *Tilapia* species are abundant in the river near the end of the dry season, but disappear at the start of the rains, being found to some extent in the shallows. This may be caused by lack of oxygen, but it could also be a breeding movement. The fisheries department of the Gold Coast (Anon 1952) has reported Nile perch floating helplessly down the River Kamba after heavy rain; deoxygenation of the water was put forward as a possible cause.

Johnels (1954) advances the theory that the flood permits rapid feeding and growth by fish because it brings various organisms with the rain water into the river and because 'the river is possibly fertilized by substances from land which will indirectly add to the production of the river'. This is probably true as far as predatory fish are concerned, but the rains dilute the plankton of the Sokoto to such an extent that for plankton-feeding fish the floods must be regarded as a time of impoverishment. This may be the cause of the slow growth of *Tilapia* species in the area, a subject to be discussed in a later paper. Le Roux (1956) showed the preference of small *Tilapia* for zooplankton. The species he worked with are not the same as those in the River Sokoto at Birnin Kebbi, but are closely related in feeding habits. Daget (1956) observed *T. zillii* (Gerv.) of 25-30 mm length with their stomachs full of copepods on 23 June in the River Niger. During the floods he found similar fish filled only with filamentous algae; he gives no date for this latter observation. The data from the Sokoto do not contradict Daget's observations. Copepods are abundant in June, and there may be a similar outburst of filamentous algae in the Middle Niger as there is in the Sokoto. *Tilapia* breed at the beginning of the rains so that the fry are subjected to a period when the plankton is greatly diluted and their preferred food item is at a very low concentration. The data for the whole year suggest that the river is not very productive. This means that for fish that are entirely plankton feeders growth will be severely limited throughout their life cycle, and this appears to be so in *T. galilaea* (Artédi), a phytoplankton feeder, which is the commonest species in the area.

ACKNOWLEDGMENTS

We wish to thank the Medical Officers in charge of the Government Hospital at Birnin Kebbi during 1954 to 1957 and Dr J. Haworth, the Officer-in-Charge of the Western Sokoto Malarial Control Project, for permission to use their records of rainfall and air temperatures, and Dr E. Lind of Makerere College, Kampala, Uganda, for examining the phytoplankton samples.

One author (M. J. H.) owes much to the unpaid assistance of his wife without whose help many of the observations could not have been made, and we both express our appreciation to Dr B. M. Gilchrist for her helpful criticisms of the manuscript.

SUMMARY

1. Two stations were sampled in the River Sokoto, Nigeria, near Birnin Kebbi, one in the main stream the other in a pool isolated during the dry season.

2. Birnin Kebbi has one wet season each year.

3. Approximately monthly data over 3½ years are given for water level, temperature, pH, alkalinity, oxygen and transparency. Samples were also taken for chemical analysis, phytoplankton and zooplankton.

4. Water temperatures tend to follow air shade minima. Nutrients, especially sulphate, are low, but calcium is abundant and pH and alkalinity usually high. Oxygen rarely falls to levels lethal to fish. Transparency is high at the end of the rains and falls to a minimum due to plankton at the end of the dry season. Differences between river and pool are attributed to evaporation.

5. Phytoplankton is scarce except from March to June and more abundant in the pool than the river.

6. Rotifera, Cladocera and Copepoda are most abundant in the dry season, Rhizopoda during floods. Differences between years are attributed to differences in nutrients and phytoplankton.

7. The zooplankton is sparse compared with that of the Illinois River and the Blue Nile.

REFERENCES

Anon. (**1952**). *Report of the Fisheries Department, Gold Coast*, for the year 1950-51, 1-11.

Beauchamp, R. S. A. (**1953**). Sulphates in African inland waters. *Nature, Lond.* **171,** 769-71.

Blanc, M., Daget, J. & d'Aubenton, F. (**1955**). Recherches hydrobiologiques dans le bassin du Moyen Niger. *Bull. Inst. franc Afr. noire.* (A), **17,** 680-746.

Cohn, L. (**1903**). Untersuchungen über des Plankton des Lowentin und einiger anderer Seen Masurens. *Z. Fisch.* **10,** 201-331.

Comita, G. W. (**1956**). A study of a calanoid copepod population in an Arctic lake. *Ecology*, **37,** 576-91.

Daget, J. (**1956**). Mémoires sur la biologie des Poissons du Niger moyen. II. Recherches sur *Tilapia zillii* (Gerv). *Bull. Inst. franc. Afr. noire* (A), **18,** 165-223.

Daget, J. (**1957**). Données récentes sur la biologie des Poissons dans le delta central du Niger. *Hydrobiologia*, **9,** 321-47.

Fish, G. R. (**1956a**). Chemical factors limiting growth of phytoplankton in Lake Victoria. *E. Afr. Agric. J.* **21,** 152-8.

Fish, G. R. (**1956b**). Some aspects of the respiration of six species of fish from Uganda. *J. Exp. Biol.* **33,** 186-95.

Fryer, G. (**1957**). The food of some freshwater cyclopoid copepods and its ecological significance. *J. Anim. Ecol.* **26,** 263-86.

Johnels, A. G. (**1954**). Notes on fishes from the Gambia River. *Ark. Zool.* (2) **6,** 327-411.

Kofoid, C. A. (**1908**). The Plankton of the Illinois River, 1894-1899, with introductory notes upon the hydrography of the Illinois River and its basin. Part II. Constituent organisms and their seasonal distribution. *Bull. Ill. Lab. Nat. Hist.* **8,** 1-361.

Komarovsky, B. (**1953**). A comparative study of the phytoplankton of several fishponds in relation to some of the essential chemical constituents of the water. *Bull. Res. Coun. Israel*, **2,** 379-410.

Le Roux, P. J. (**1956**). Feeding habits of the young of four species of *Tilapia*. *S. Afr. J. Sci.* **53,** 33-7.

Macan, T. T. (**1958**). The temperature of a small stony stream. *Hydrobiologia*, **12,** 89-105.

Mortimer, C. H. (**1949**). Seasonal changes in chemical conditions near the mud surface in two lakes of the English Lake District. *Verh. Int. Ver. Limnol.* **10,** 353-6.

Rzóska, J., Brook, A. J. & Prowse, G. A. (**1955**). Seasonal plankton development in the White and Blue Nile near Khartoum. *Verh. Int. Ver. Limnol.* **12,** 327-34.

Steur, A. (**1901**). Die Entomostrakenfauna der 'alten Donau' bei Wien. *Zool. Jb. (Syst.)*, **15,** 1-156.

NATURAL FEATURES AND BLOWFLY MOVEMENT

By JOHN MACLEOD and JOSEPH DONNELLY

Ministry of Agriculture (Animal Health Division), Field Research Laboratory, Blackford, Carlisle

(With 1 Figure in the Text)

We have previously shown (MacLeod & Donnelly 1958), that blowflies dispersing in a given direction are not deterred by a ground slope of 45° rising 500 ft. In the present paper we describe field experiments which revealed similar absence of any barrier effect when released populations of blowflies encountered an expanse of water and a belt of trees athwart the field of dispersal from the initial concentration.

The numbers of the predominant species or species groups in the test areas are estimated by the method suggested elsewhere (MacLeod 1958) for this type of low-incidence recovery data. The estimations serve incidentally to illustrate how the method may be adapted to fit particular cases.

THE RIVER-CROSSING EXPERIMENT

A test was made of the possible barrier effect against spread of blowflies offered by the 200-yd width of the River Eden, immediately before it enters the Solway estuary. This width was considered to be sufficient to preclude the possibility of a blowfly being aware of the far bank, when its flight crossed the line of the water edge. There was of course no reason to doubt the physical ability of a blowfly to cover 200 yd in one flight. If, however, the flies could not foresee the end of a flight out over water, the extent to which such flights ended in a crossing should indicate whether flight direction was or was not affected by the nature of the terrain below. From the practical point of view, it is to be remembered that the great majority of streams in Great Britain are less than 100 yd broad; watercourses can therefore be of importance in limiting movement of blowfly populations only if relatively narrow stretches of water are effective barriers.

In the test area, immediately seaward of the village of Rockcliffe, the river runs due west through alluvial plain. The ground to the south is marshy—'saltings'—with grazing fields. On the north are the policies of a private estate, semi-arable, with grazing fields and occasional wood. The ground is slightly higher and rather more fertile than on the south side of the river.

Blowflies were trapped on Crosby aerodrome, made radioactive by addition of ^{32}P to their drinking water (MacLeod & Donnelly 1957a) over a period of 36 h, and released on the south bank of the river on the evening of 14 August. Six groups of twelve traps were put out, two at approximately $\frac{1}{4}$ mile, two at $\frac{1}{2}$ mile, and two at 1 mile from the release point (R.P.), and arranged as indicated in Fig. 1*a*. Across the river three rows of twelve traps were placed in lines parallel to the bank, the first near the water edge, the second about 30 yd back, at the foot of a

wooded bank. The third, about 40 yd still further back, was on a mown hayfield above the bank. The traps in each row were 25 yd apart; thus they covered an area directly opposite the release point of approximately 300 yd frontage and 70 yd in depth. These nine sets of traps were put out before the marked flies were released. Within a half-hour after release, a further set of twelve traps was put out in three rows of four traps, 15 yd apart, covering the release area. All traps were baited with minced herring. Trapping continued until 20 August, the traps being changed and bait renewed daily. The net release of active blowflies consisted of 484 *Lucilia caesar* group (*L.c.* gp.), 1339 *Calliphora erythrocephala*, and 74 *C. vomitoria*.

Almost continuous rain, with low air temperatures, resulted in disappointingly low total catches, and the experiment was further bedevilled by the continuous interference, probably by foxes, with certain trap lines, notably set 3, which had ultimately to be discontinued. However, 19 and 82 marked specimens of *L.c.* gp. flies and of *C. erythrocephala* were recovered. Of these 8 and 41 were taken across the river, indicating that for these species 200 yd of water was not an effective barrier. No *C. vomitoria* was recovered.

Unfortunately the recovery trapping results in the release area itself were irregular, from interference with the traps, and so the significance of the proportion caught 200-300 yd away across the river is difficult to assess. If, however, recoveries trapped at different distances from the release point are expressed as recoveries per 100 trap-days, we have:

Trap sets	Distance (miles)	Traps × days	Recoveries per 100 trap-days	
			L.c. gp.	*C. erythrocephala*
8, 9, 10	$\frac{1}{8}$	213	4	20
2	$\frac{1}{4}$	58	2	33
4, 6	$\frac{1}{2}$	122	0·8	3·3
5, 7	$\frac{3}{4}$	133	1·5	3

From the relative recoveries at one-eighth mile there is no evidence that the water stretch in this instance had an appreciable barrier effect on the northwards dispersal of the released concentration.

The local population density

From the data some estimates of density of blowflies may be made, by the approximate method described for other blowfly work (MacLeod 1958). The traps at the release point occupied an area of 30 × 45 yd. Assuming this to be a circle of 25 yd radius, 'the equivalent zone of influence' has a radius of 125 yd (extending half-way into a surrounding annulus which is 'one unit of fly territory' in width—200 yd), *i.e.* is approximately 10 acres.

L.c. gp.: 484 released; less 2% death rate for one day, 474. Sample and recoveries in the release area on Day 1 were 8 and 7, *i.e.* on a straight Lincoln Index basis density equals 542 flies or 54 per acre. If 4% death rate is allowed, the estimate is 53 per acre. Similarly with *C. erythrocephala*, the estimates are 186 and 182 per

acre. These ignore dispersal of many of the released flies beyond the confines of the 10-acre zone sampled by the traps. It is assumed that an average of 16% are available to a fully trapped unit of territory ($\pi.100^2$ yd), over the first week after release. The zone of influence for such traps would be 25 acres ($\pi.200^2$ yd). In the 10-acre zone of influence of the release-area traps there would be expected 10/25 of 16%, say 6% of the surviving released flies. If this proportion be taken as an estimate (almost certainly low) of the numbers available on the first day, the density estimates become 6% of 54 *L.c.* gp. and of 186 *C. erythrocephala* per acre, *i.e.* 3 and 11. No samples of *L.c.* gp. flies were obtained in the release area after Day 1, and only three further *C. erythrocephala*, so a mid-week estimate of the population, based on pooled samples and recoveries and 6% of a calculated

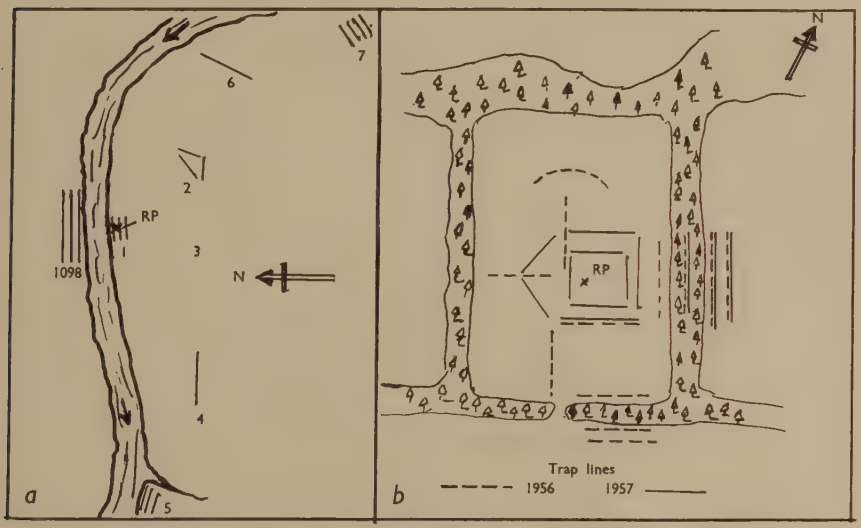


Fig. 1. *a*, The distribution of the ten trap lines at Rockcliffe; *b*, The Oakbank enclosure and trap lines. Not to scale; hedges and tracks not shown.

mean number of surviving marked flies, could obviously not differ much from the above second estimates.

The question may be further examined, however, from the results for the north bank trapping area. The traps were distributed over a rectangle 300 yd long and from 200 to 275 yd away from the R.P., so that they lay within the first annulus of territory units round the central release unit. Within this annulus there is assumed to be at midweek approximately 3·3/19 of the available marked flies. The annulus being approximately 6 units, a unit of territory in the annulus will thus contain approximately 1/40 of the available flies. Assuming the trapped rectangle to correspond roughly to a circular area of 100 yd radius, *i.e.* a unit of territory, it will itself contain 1/40 of the availables, and the traps will have an equivalent zone of influence of four times the trapped area, since trapped area/zone

of influence = $\pi.100^2, \pi.200^2$. Of the trap-influenced annulus round the trapped unit, the arc nearest the R.P. will presumably have a higher density, and the furthest away arc a lower, than the central trapped unit of territory. If we assume that the average density in the annulus is approximately the same as that in the central unit, then the traps in the north bank area should sample 4/40, or 10% of the available population. We may now estimate the midweek population on the north bank. The method is as follows: Allowing 2% wastage rate per day after deducting recaptures, daily numbers available are calculated, and a mean value for the 6 days taken. For *C. erythrocephala* this is 1198 (1116 with a 4% loss rate). The total samples and recoveries (247 and 41) and 10% of the average of survivors, viz. 120, give an estimate of 730 for 25 acres (the equivalent zone of influence of a fully trapped unit), or 29 *C. erythrocephala* per acre. At 4% loss rate the estimate is 27. Similarly with the *L.c.* gp. flies: average of survivors equals 438 (409). Total samples and recoveries 109 and 8, density estimate per acre 24 (22).

The total recoveries to total samples over the whole experiment were 19 to 188 *L.c.* gp. (10.1%), and 82 to 779 *C. erythrocephala* (10·5%). This would suggest that the *L.c.* gp.: *C. erythrocephala* ratio in the population was approximately the same as that in the marked flies, which was 484 : 1339, say 3 : 8. On the north bank, the recoveries : samples ratios were 1 : 14 for the *L.c.* gp. and 1 : 6 for *C. erythrocephala*, whereas over the remainder of the area they were 1 : 7 and 1 : 13. The ratios over the whole experiment being 1 : 10 for both the *L.c.* gp. and *C. erythrocephala*, it follows that *L.c.* gp. flies were relatively more numerous on the north bank and *C. erythrocephala* on the more marshy ground to the south, a conclusion in accord with expectations from our knowledge of the habitat relations of the two genera.

The actual recoveries to total samples were:

North bank	*L.c.* gp.	8 : 109	*C. erythrocephala*	41 : 247
South of river		11 : 79		41 : 532

That is, the *L.c.* gp. : *C. erythrocephala* ratios in the recoveries are about 1 : 5 and 1 : 4. But these may well be affected by difference in likelihood of trapping of *C. erythrocephala* and *L.c.* gp. flies. The true ratio in the marked population is 484 : 1339, or approximately 3 : 8. Assuming that the two groups of flies crossed the river equally readily, we may convert the total sample values to relative values on the above basis:

	L.c. gp.	*C. erythrocephala*	*L.c.* gp.: *C. erythrocephala* in natives
North bank	3 : 41	8 : 50	41 : 50
South of river	3 : 21	8 : 106	21 : 106

These should represent the true *L.c.* gp.: *C. erythrocephala* ratio not biased by differences in trap response. The *L.c.* gp.: *C. erythrocephala* ratio would thus seem

to be 4 : 5 on the north bank (compare estimates 24 *L.c.* gp. and 29 *C. erythrocephala* per acre), but only 1 : 5 on the south. The Day 1 estimates of 3 and 11 for the release area thus probably reflect the true relative order; an estimate of the absolute values depends on the unknown proportion of the surviving releases still within the influence of the traps during the first day.

THE WOOD-PENETRATION EXPERIMENT

As with an expanse of unfavourable terrain below, so with an abrupt change of sub-aerial conditions, the question arises whether the direction of a flight, commenced over open terrain, is affected by encounter with a stand of tall vegetation.

A rectangular area of arable and grass fields (Fig. 1*b*), about $\frac{1}{2} \times \frac{3}{8}$ mile, on the farm of Oakbank, near Longtown, was the venue for a test of this question in October 1956. At this time, with fields bare and the grass close-cropped, the area was almost entirely the open-ground formation type of Elton & Miller (1954), and restricted vertically to their ground-zone layer. Surrounding the area was a fringe of wood. On the north-east side this formed a belt of fairly uniform density, mainly deciduous, and about 90 yd wide; on the south-east side the belt was similarly of a uniform depth and density, but mainly spruce, and about 50 yd wide. On both sides the transition to woodland was abrupt. The woodland was high-canopy, with rather more low-canopy scrub and tall-field-layer growth in the north-east wood belt.

Local blowflies were trapped on 9 October, dusted with dye powder and released at noon on 11 October at a point about 250 and 400 yd from the north-east and south-east boundaries of the enclosure. At this late season few flies of species other than *C. erythrocephala* were trapped. The net viable release was: *L.c.* gp. 15, *C. erythrocephala* 385, *C. vomitoria* 7. The flies were all females. In addition a number of laboratory-bred *Lucilia sericata*, experimentally treated, were released at this point in connection with a different investigation. Immediately before and after the release, the recovery traps were put out. Within the enclosure seven trap lines of ten traps were distributed at varying distances from the R.P. An eighth was placed in a ride in the north-east wood, and two in a stubble field beyond this wood, 25 and 50 yd out respectively. Two trap lines were placed in a grazing field 10 and 40 yd respectively beyond the south-east wood belt. Trapping was discontinued on 15 October.

Twenty-five *Calliphora erythrocephala* flies were recovered. Of these 18 were taken in the seven trap sets within the enclosure, 2 in the set within the wood, 1 and 4 respectively in the first sets beyond the wood to the north-east and south-east. Unexpectedly, 2 of the 7 *C. vomitoria* releases were recovered; both were in the first trap line beyond the wood to the south-east. Of the laboratory-bred and experimentally treated *L. sericata*, 19 were recovered, 16 being in the three trap lines nearest to the R.P. Of the remaining 3, 1 was beyond the north-east wood.

The experiment was repeated at the end of August of the following year, at which time the rank growth of the hedgerows and field borders in the enclosure represented an appreciable addition of field-formation type to the open-ground

type of the actual fields. The initiation coincided with the beginning of a spell of unfavourable weather, and after 5 days' trapping it was possible to release only the meagre total of 152 *L.c.* gp., 216 *C. erythrocephala* and 30 *C. vomitoria*. For recovery trapping, nine sets of twelve traps were used inside the boundary, in two concentric circles round the R.P.; a tenth was placed as before in the transition 'wood-edge' represented by the ride in the north-east wood, and two in the field (again stubble) beyond the wood. Recovery trapping was continued for 7 days after release, but because of almost continuous drizzle alternating with strong wind there was very little fly activity. Four *L.c.* gp. flies were recovered in each of the inner and outer circles of traps round the R.P., representing in each case approximately 1% of the total *Lucilia* spp. catch. No marked flies were recovered from the wood trap line, but in the two trap lines beyond the wood 2 marked *L. caesar* among 102 *L.c.* gp. flies were taken. Similarly, 2 marked *C. erythrocephala* were taken in 149 flies, as opposed to 13 (2%) and 17 (1·7%) in the inner and outer rings around the R.P. There is no suggestion from these tests of any restrictive effect on movement of either *C. erythrocephala* or *C. vomitoria*, or of either *L. sericata* or *L. caesar*, from the presence of a wood belt 50 yd or more wide.

Population structure at Oakbank

In the 1957 test, as in the earlier one, a number of groups of laboratory-bred *L. sericata* were released at the same time as the wild material, in a test of the biological effects of irradiation and other treatments. One group was an untreated control, and the recoveries of this group, with those of the wild flies, allow estimates of numbers within the enclosed area.

The traps covered an area of approximately 250 × 400 yd. Allowing, as before, a belt 100 yd wide around this, we have an 'equivalent zone of influence' of the traps of 450 × 600 yd, or approximately 56 acres, which is equivalent to the central unit area and the whole of the first surrounding annulus of territory units of a release point. The net release of *L. sericata* was 1003; 11 were recovered, along with 2 native *L. sericata*. Assuming a 4% loss of this laboratory-bred material, the midweek estimate of surviving marked *L. sericata* is 860, of which 37%, or 318, are assumed to be within the equivalent zone of influence at midweek. The estimate of the total *L. sericata* population, 318 × 13 11. = 376 for the 56 acres, giving a native *L. sericata* estimate of 58, or 1 per acre.

The total *L.c.* gp. catch for the nine sets of traps was 840, of which 8 were marked. Release was 152, with a total of 10 recaptures: the midweek estimate of survivors for 2% loss rate is 138 (for 4%, 129). With 37% of these assumed to be available to the traps, the estimate is 5380, or 96 (90) per acre. Similarly for the *C. erythrocephala* estimate: 210 females released, 29 recovered in a total sample of 1346, giving an estimate of 57 per acre. Only 6 males were released, of which one was recovered in 283 flies, an estimate of 10 per acre.

The higher density of *Lucilia* spp. than of *C. erythrocephala* is doubtless related to the sheltered nature of the enclosure, and the presence of field layer vegetation interspersed with the open-ground type of the grazing and stubble fields. As was

found in the Crosby work (MacLeod & Donnelly 1957b), the species structure changes markedly in the late season, owing to the earlier seasonal decline of the *Lucilia* than the *Calliphora* component. The proportions in the recovery trappings in early September (1957) and in October (1956) were:

	C.e. %	*C.v.* %	*Lucilia* spp. %
September	54	15·5	28
October	86	10	3·5

Within the *Lucilia* spp. group the *L. caesar* : *L. illustris* ratio was 10 : 7 in early September, but 10 : 1 in October. *L. sericata*, which appears to be more susceptible than the other species to weather conditions unfavourable for activity, was practically absent from the September catches. The other less common blowfly species, except *L. silvarum*, showed little difference. The numbers (males/females) were:

	September	October
Lucilia sericata	–/2	5/36
L. ampullacea	3/79	–/96
L. silvarum	10/84	3/7
Calliphora loewi	1/14	–/25
Acrophaga subalpina	2/2	1/2
Cynomyia mortuorum	34/27	28/46
Phormia terrae-novae	2/2	1/1

DISCUSSION

In an earlier paper (MacLeod & Donnelly 1958) we recorded observations on the dispersal paths of an artificial concentration of blowflies, showing that the flies dispersed in all directions, irrespective of suitability of habitat. If this be taken as the normal behaviour pattern in the dispersal of natural groupings, it would imply a fairly regular distribution in nature, and would give a biological meaning to estimates of mean density over large areas. In fact, the natural blowfly population is characterized by an extreme patchiness of distribution (MacLeod 1956, MacLeod & Donnelly 1957b, and unpublished work). To reconcile these findings we suggested that the mosaic nature of the population distribution is not due to the 'deliberate' selection of their habitat by the wandering individual flies, through a succession of avoidance deflections of flight line on encountering less favourable habitat. Where an undirected flight happens to reach highly favourable territory, the chances of the flight being interrupted by positive tropotactic stimuli are greater, and also an orthokinetic slowing down occurs. The population thus shows bunching within a favourable habitat into a pattern of density peaks and depressions, the peaks being related to the frequency of sources of attraction. The work reported here throws further light on the mechanism of aggregation.

It was found that both *L. caesar* group flies and *C. erythrocephala* readily crossed 200 yd of water. It might be objected that there is no proof that the blowflies at the start of the crossing flight were unable to identify as favourable the terrain across the river; it is obvious, however, that they should equally be able to recognize the unfavourable nature of the intervening stretch of water. Similarly with the wood barrier test, *Lucilia sericata*, a 'sun-loving' species, entered,

penetrated and emerged from a 90-yd wood belt, as did *L.c.* gp. and *Caliphora erythrocephala* flies. *C. vomitoria*, a wood-haunting species, penetrated a 50-yd wood belt, to emerge again into the open. The transition from the open ground to the woodland was abrupt, and there is no doubt that the change in environmental stimuli was dramatic. In both the deciduous and the coniferous wood the sky radiation would have been only about 5%, certainly no more than 10%, of that in the open (Ovington & Madgwick 1955). The temperature would have been distinctly lower (Geiger 1950) under outdoor conditions warm enough to permit flight, and the air humidity, receiving contributions both from the canopy and the ground, would have been higher, particularly at about 3 m, in the 'tree-trunk' zone, through which presumably the flies passed. The humidity difference may have been less marked for the September wood test than would ordinarily be expected, because of the high rainfall at the time, but it would certainly have been present during the longer dry and warm intervals, when presumably much of the fly movement took place. It is possible that the *Lucilia sericata* specimen, and the *Calliphora erythrocephala* flies, which also favour open rather than shaded habitat, flew over instead of through the wood. This does not affect the significance of the result. A klinokinetic response to a change of environment assumes the existence of a reflex, conditioned by racial experience; by this same experience the airborne fly would be expected to recognize an unfavourable habitat below as well as in front. The presence of carrion bait beyond the wood, and beyond the river, cannot have been an overriding stimulus, as in both cases the adventurers started from a bait-trapped environment.

The observations support the thesis that aggregations of blowflies, within their major habitat areas, are not a result of directed travel by the individuals, but are due to different degrees of attraction to loiter offered to these individuals as in their aimless dispersal movements they blunder across different activity arenas. From the *ad hoc* point of view the results, and the earlier reported failure of a very steep hill-face rising 500 ft to stop the spread of blowflies, offer little hope that natural features are at all likely to act as barriers, in Britain at least. A high local concentration, resulting from a recent temporary abundance of carrion, as for example from flood casualties, or from a local epidemic among wild fauna, would affect a much wider area than if the individual flies were 'territorially bound' to the population centres, or even to the major habitat areas, in which they originated. Similar independence of the habitat traversed has been shown for the American blowfly, *Phormia regina*, released groups of which travelled up to 10 miles, undeterred by the hilly terrain, with wooded ridges and watercourses (Schoof & Mail 1953).

SUMMARY

1. Marked *Lucilia caesar* group and *Calliphora erythrocephala* blowflies released beside a 200-yd wide river were recaptured in numbers on the far side.

2. In two late-summer and autumn tests of the barrier effect of a deciduous wood belt 90 yd wide, *Lucilia sericata*, *L. caesar* and *Calliphora erythrocephala*

were recovered beyond the wood; *C. vomitoria* was recovered beyond a 50-yd wide stand of conifers.

3. Estimates are given of the density in the test areas of some of the species concerned.

4. The bearing of the observations on dispersal theory is briefly discussed.

REFERENCES

Elton, C. S. & Miller, R. S. (1954). The ecological survey of animal communities: with a practical system of classifying habitats by structural characters. *J. Ecol.* **42,** 460-96.

Geiger, R. (1950). *The climate near the ground.* Cambridge, Mass.

MacLeod, J. (1956). A preliminary experiment on the local distribution of blowflies. *J. Anim. Ecol.* **25,** 303-18.

MacLeod, J. (1958). The estimation of numbers of mobile insects from low-incidence recapture data. *Trans. R. Ent. Soc. Lond.* **110,** 363-92.

MacLeod, J. & Donnelly, J. (1957a). Individual and group marking methods for fly-population studies. *Bull. Ent. Res.* **48,** 585-92.

MacLeod, J. & Donnelly, J. (1957b). Some ecological relationships of natural populations of calliphorine blowflies. *J. Anim. Ecol.* **26,** 135-70.

MacLeod, J. & Donnelly, J. (1958). Local distribution and dispersal paths of blowflies in hill country. *J. Anim. Ecol.* **27,** 349-74.

Ovington, J. D. & Madgwick, H. A. I. (1955). A comparison of light in different woodlands. *Forestry,* **28,** 141-6.

Schoof, H. F. & Mail, G. A. (1953). Dispersal habits of *Phormia regina* in Charleston, West Virginia. *J. Econ. Ent.* **46,** 258-62.

FACTORS INFLUENCING GROWTH-RATE IN *BALANUS BALANOIDES*

By D. J. CRISP

Marine Biology Station, Menai Bridge, Anglesey

(With Plate 3 and 5 Figures in the Text)

The rate of growth of the common shore barnacle of boreal coasts, *Balanus balanoides* (L.), has been investigated at a number of localities by different workers. The literature has been critically reviewed by Barnes & Powell (1953), who concluded that the seasonal changes in rate of growth were similar over the whole of its range. Nevertheless, the actual rates of growth vary considerably as can be seen from the summary of earlier work given in Table 1, in which growth-rates are compared on the basis of size attained at the end of the first year. Only a limited study has been made of the factors controlling growth in any one given area. The influence of the tidal level at which the barnacle grows has been shown by Hatton & Fischer-Piette (1932), by Moore (1934) and by Barnes & Powell (1953) to be of importance, those individuals able to feed for a longer period at the level of low water growing faster than those living at high water. Barnes (1953) investigated growth-rates at different light intensities, and concluded, notwithstanding the observations of Klugh & Newcombe (1935), that light was without influence. In further measurements on specimens immersed continuously from a raft, Barnes (1955) found that the presence of competing organisms seriously interfered with growth especially in its early stages soon after settlement. Hatton & Fischer-Piette (1932) compared growth-rates at stations in the same locality differing in their exposure to wave action, and found that growth was greatest at exposed localities, a conclusion also reached by Moore (1934) in the Isle of Man. Moore (1936) found that, at localities near Plymouth, growth was greater where there was a current of water containing suspended matter than at more exposed localities with clear water in the same area; Hatton (1938) demonstrated the advantage of water flow in the St Malo area by transplanting individuals on rock from a stagnant area to one where they were in the path of tidal currents. Moore (1934, 1958) found some evidence that crowded individuals grew more slowly, but his findings may be criticized on two grounds; first that one of the isolated individuals with which the crowded ones were compared could clearly be seen in the original plate to be *Chthamalus stellatus*, secondly because the crowded group had settled in a shallow groove which, as Hatton (1938) later demonstrated, would itself retard growth.

It is convenient to divide the factors influencing growth-rate into two groups, regional and local. Regional environmental factors include the temperature and salinity of the water and its richness in suspended nutrients, while local environmental factors include the flow of water over the barnacle, the orientation of the

barnacle in relation to water flow, the population density of surrounding individuals and the presence of parasites. *Balanus balanoides* is not a suitable animal for the study of the effects of regional factors in the field because, on account of its short period of settlement, all individuals of a single year-group grow under the same sequence of changes in the regional environment. On the other hand, its short period of settlement makes it useful for studying the influence of the various local factors, because, in the absence of further settlement of the species, all individuals

Table 1. *Growth rates of* Balanus balanoides *in various localities*

Locality and observer	Approx. mean monthly temperature (° C) Min. (Feb.) Air	Min. (Feb.) Sea	Max. (July) Air	Max. (July) Sea	Conditions of experimental barnacles measured	Mean rostro-carinal diameter at end of first year
Herdla, Norway (Runnström 1925)	4·1	4·4	14·1	13·3	Isolated intertidal specimens	7-9 mm
Millport, Scotland (Barnes & Powell 1953)	5·2	6·8	14·4	13·4	Isolated individuals	
					Upper littoral	10 mm
					Mid-littoral	13-14 mm
					Lower littoral	15 mm
					Submerged on raft	17·5 mm
Port Erin, Isle of Man (Moore 1934)	5·7	6·9	14·9	13·7	Isolated individuals	
					Upper littoral	5·2 mm
					Mid-littoral	5·3 mm
					Lower littoral	4·7 mm
Liverpool (Corlett 1948)	5·0	5·0	15·8	16·4	Individuals growing on piles on River Mersey	5·9 mm
Menai Straits, North Wales (this investigation)	6·1	5·0	15·6	15·4	Isolated individuals submerged on raft	
					Greatest current	17 mm
					Least current	12 mm
Luc sur Mer, France (Topsent 1911)	6·4	7·0	16·8	17·0	Natural population* on *Mytilus* and stones at low water	5-6 mm by July
St Malo, France (Hatton & Fischer-Piette 1932)	6·6	7·5	16·8	17·5	Natural populations at several levels and exposure conditions	2·5-4 mm

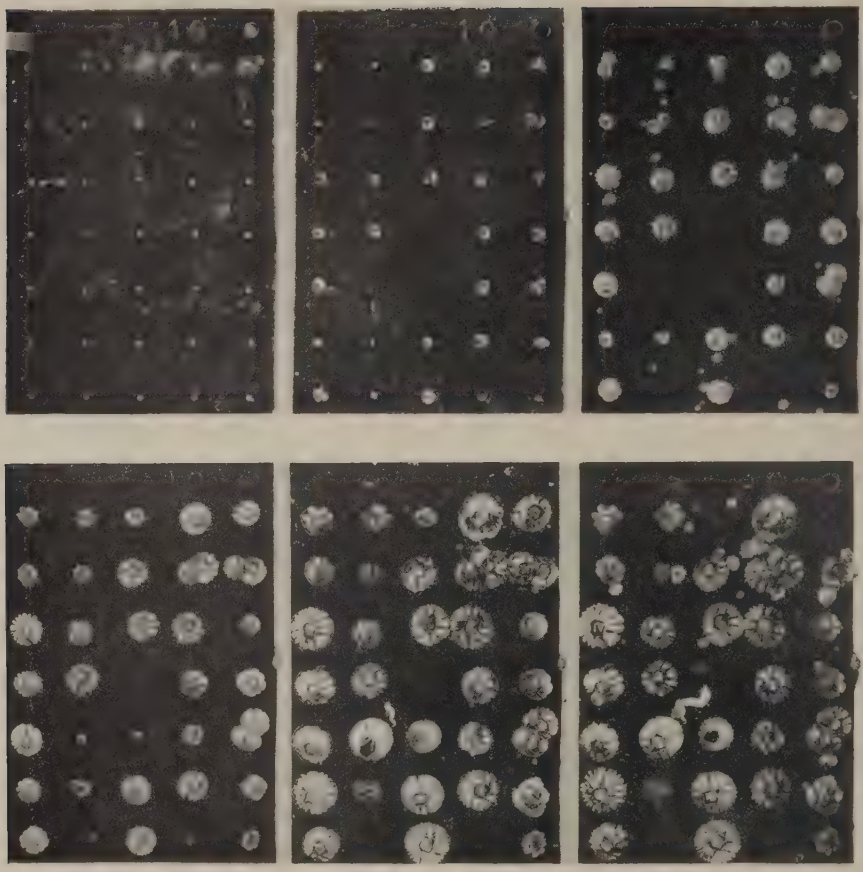
* Identified as *B. crenatus* but appear to be *B. balanoides* from photographs.

The sea and air temperatures quoted in this table were derived from various sources including U.S. Navy *Marine Climatic Atlas of the World*, I, Washington, D.C., 1958; *The Advanced Atlas of Modern Geography*, Bartholomew, 1953; *World Atlas of Sea Surface Temperatures*, Hydrographic Office, U.S. Navy, Washington, D.C., 1944; and from locally available data on sea and air temperatures. The values quoted are not therefore derived from corresponding data, and are intended only as an approximate indication of prevailing conditions.

must grow under otherwise closely corresponding conditions. In this paper the effects of local environmental factors as enumerated above have been systematically studied on barnacles fixed to a raft in the Menai Straits and continuously immersed.

EXPERIMENTAL PROCEDURE

Small rectangular panels of 'Tufnol' laminated phenol-formaldehyde resin measuring 15×10 cm were prepared to receive settlement by drilling small



Sequence of photographs of panels bearing regularly arranged specimens of *Balanus balanoides* to show growth. Note in the lower row of photographs four specimens of *Elminius modestus* (top left) and two specimens of *Balanus crenatus* (just below the tubeworm *Pomatoceros triqueter*) which settled after *Balanus balanoides*.

(*Facing p.* 97)

hemispherical pits on the surface with a dentist's bit of about 1·5 mm diameter. This method had the advantage over that used in earlier experiments (Crisp & Barnes 1954) that there was no tendency for a lip to be left overhanging the pit; the edge of the pit was cleanly cut and the surface of the pit could be made quite smooth. Pits were drilled in equidistant rows intersecting at right angles, with the pits separated by 0·5, 1·0 and 2·0 cm respectively in each of three series of panels. When these panels were placed on pier piles at low water mark the cyprids settled almost entirely in the pits, so that the resulting densities were very close to 4, 1 and 0·25 individuals per cm^2 respectively on each of the three series of panels. By exposing the panels near the end of the settling season in the middle of May, there was little tendency for further settlement of *B. balanoides*, and cleaning off superfluous spat was kept to a minimum. When sufficient numbers had settled, and all, or nearly all, the pits were filled, the panels were inspected in the laboratory. Superfluous spat were taken off with a needle to leave one in each pit, unless it was thought that the remaining individual might also be damaged in the process, and photographs were taken of each of the panels. The panels were then screwed in position on a heavy wooden board, to which swivels were attached so that it could be moored in a vertical position and could swing with the tide as described elsewhere (Crisp & Stubbings 1957).

The barnacles on each panel had settled with a tendency to orientate in one direction, towards the light (Barnes, Crisp & Powell 1951). When fixing the panels to the board, they were arranged so that each series of panels containing population densities of 4, 1 or 0·25 individuals per cm^2 had in all a roughly equal representation of individuals set along, against and across the direction of the water current. As the experiment proceeded, the panels bearing a majority of individuals with their axes across the current needed some readjustment in position because of the rotation of the rostro-carinal axis produced by unidirectional flow of water over them (Crisp 1953, Crisp & Stubbings 1957). The experimental arrangement of the panels is shown in Table 2. It will be seen that on the surfaces A, B and C are represented one each of the three population density series, and that they have been arranged in a balanced design not only in respect of the major direction of orientation but also in their order from the leading edge of the board. The three panels on surface D formed a separate comparison; on this surface the panels were separated by baffles 2·5 cm high to interrupt the free flow of water over the surface, but otherwise the panels were similarly treated to those on surfaces A, B and C.

The panels were withdrawn and photographed at intervals, all extraneous growth and later spat being removed by scrubbing or prising off with a needle. An exception was made only where an individual had been accidentally lost. It was considered best in such cases to allow individuals of a later settling species, either of *Elminius modestus* or of *Balanus crenatus*, which settled in the empty pits, to take the place of any *B. balanoides* lost from the population and so to maintain it at its former density. Plate 3 shows a typical series of photographs which were available for analysis at the end of the experiment. Except on the last occasion, the panels were replaced in the sea on the same or on the following day. After

the final series of photographs of each panel had been taken, a print was made on which each individual was numbered. The barnacles were then removed, superfluous water blotted off on filter paper, and each individual weighed on a torsion balance to the nearest 10 mg, the weight being tabulated against its number. In some cases, the length, breadth and height were also measured and the weight of the egg masses or of parasites present recorded separately. The weights were found to afford a more convenient, more accurate and more sensitive indication of growth than could be obtained from photographs or from linear measurements.

INFLUENCE OF PARASITISM ON GROWTH

When the barnacles were removed at the end of the experiment, 1·7% of all individuals were found to have become infected by the isopod *Hemioniscus balani*

Table 2. *Experimental arrangement of panels on swivelled board, and mean weights of barnacles growing on each panel*

Surface	Part of board used	Approximate density of population		
		4·0/cm²	1·0/cm²	0·25/cm²
A	Port side	No. 4 β + 0·590 g	No. 5 α ~ 0·573 g	No. 10 γ − 0·544 g
B	Starboard side, uppermost row of panels	No. 2 α − 0·589 g	No. 6 γ + 0·780 g	No. 9 β ~ 0·832 g
C	Starboard side, lowest row of panels	No. 1 γ ~ 0·539 g	No. 8 β − 0·641 g	No. 11 α + 0·826 g
D	Starboard side, panels separated by baffles	No. 3 γ ~ 0·389 g	No. 7 β ~ 0·489 g	No. 12 α ~ 0·301 g

α, β, γ Refer to the order in which the panels were placed, α being nearest and γ furthest from the current source.

+, ~, − Refer to the orientation of the majority of individuals on the panel. + means that the rostrum of the majority was towards the current source, − that the carina of the majority was towards the current source, and ~ that the rostro-carinal axis of the majority lay across the direction of the current.

(Bate) during the first season of growth, though only seven out of twelve panels bore any parasitized barnacles. The parasites had an average weight of 37 mg, ranging from 110 down to 8 mg. All the infected barnacles were without egg masses except for the barnacle with the smallest parasite, but almost all uninfected barnacles contained fertilized eggs.

The effect of parasitism on growth was analysed as follows. The weight of each parasitized barnacle, including that of the parasite, was expressed as a percentage of the mean weight of all the other individuals growing on the same panel. In this way, the differences in growth-rates of barnacles on differently situated panels were eliminated from the comparison of infected and uninfected barnacles. The mean value of the percentage weight of the eighteen infected individuals in relation to normal ones on the same panel was found to be 62·3% with a standard error of

7·18%. The standard error associated with the much larger number of uninfected barnacles (823 in all) was 1·4% of the mean, so that the combined error of the differences between infected and normal barnacles was 9·47%. Applying the '*t*' test to the deficiency of 37·7% in the weight of parasitized barnacles showed a highly significant difference.

The result based on final weights was confirmed by measurements of rostro-carinal diameters of infected and of adjacent uninfected individuals. Fig. 1*a* shows that on a panel with a low density of population the growth of parasitized individuals, though practically normal up to the beginning of July, fell off sharply thereafter. On panels with more crowded populations (Fig. 1*b*) the sudden arrest of growth in July is still evident, but the effect is less marked because crowding prevented normal individuals from spreading freely over the panel surface. It will be seen that the mean diameter of the infected barnacles did not increase at

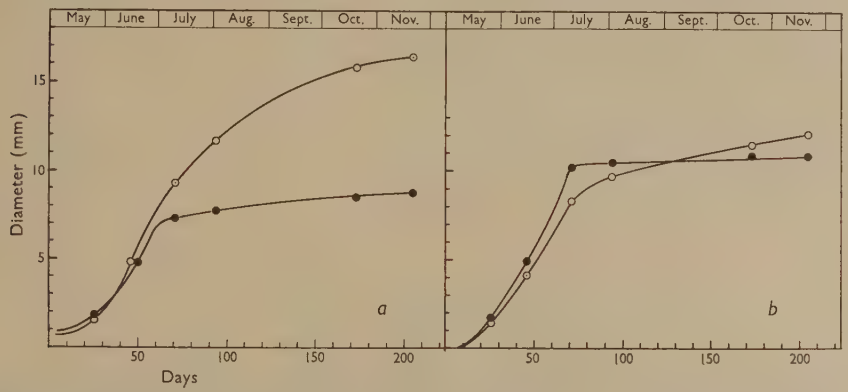


Fig. 1. Growth curves of unparasitized (—o—) and parasitized (—•—) specimens of *Balanus balanoides*: *a*, individuals on panel 9 growing at a density of 0·25/cm²; *b*, individuals on panel 7 growing at a density of 1·0/cm².

all after August; for while some grew a little, others were in fact compressed to a smaller size by the growth of surrounding healthy barnacles. Table 3 compares the diameters and weights of infected and adjacent normal barnacles present at three population densities. Surprisingly, the better-growing barnacles appeared to be the more seriously affected, even though the parasites they harboured were smaller. It is also surprising that the parasite, which on average contained less tissue weight than the ovary of a normal individual which it replaced, should have had so great an effect on the growth of the rest of the barnacle. The parasites found in these first-year barnacles were rather small immature females, or females with early embryos; hence it is unlikely that many of the parasites had previously shed larvae derived from nourishment obtained from the host. A possible explanation of the discrepancy is that the parasite is inefficient in utilizing its host's tissues, and that, since the weight of the barnacle is in large degree due to its shell, a small loss of barnacle tissue might be accompanied by a correspondingly greater

loss of shell weight. It is unlikely that *Hemioniscus* attacks only the slower-growing individuals, since there was no discrepancy in the initial growth-rate of infected individuals. The presumption is, therefore, that the parasite makes its influence felt in early July in most cases, and thereafter reduces the rate of growth of the host.

Table 3. *Comparison of parasitized and unparasitized individuals on* 21 *November* 1954

	Panel numbers		
	4	7	9 and 12
Approximate density of population	4·0/cm²	1·0/cm²	0·25/cm²
Number of parasitized specimens	6	5	3
Mean weight of parasites (mg)	50	36	24
Mean diameter of parasitized barnacles (mm)	7·8	11·2	9·4
Mean diameter of adjacent unparasitized barnacles (mm)	9·5	12·1	14·2
Mean weight of parasitized barnacles (*Wp*) (mg)	330	278	150
Mean weight of unparasitized barnacles (*Wn*) (mg)	553	516	573
Weight of parasites as percentage of weight of infected individuals	15·2	13·0	16·0
Weight of parasites as percentage of weight of adjacent uninfected individuals	9·1	7·0	4·2
Weight of egg masses as percentage of weight of adjacent uninfected individuals	13·6	11·2	10·7
Deficiency of mean weight of parasitized barnacles as percentage of weight of adjacent unparasitized barnacles (*Wn*-*Wp*)/*Wn*	40·3	46·5	74·0

VARIABILITY IN GROWTH-RATE

Omitting only parasitized individuals, the final weights of all the barnacles were first analysed to obtain the extent of variation between individuals on a given panel. Such individuals had been exposed to similar conditions except for relatively small variations in the flow régime over the panel, in population density and in their orientation to current. All had started from an initial size between that of recently

Table 4. *Variation in weight of* 1388 *individuals growing on twelve panels at the end of the experiment*

Source of variation	Degrees of freedom	Sum of squares	Mean square
Between panels	11	16·6888	1·51716
Between individuals on a panel	1376	60·9955	0·04398
Total	1387	77·6843	

settled cyprids (0·8 mm) and 7-day-old barnacles (1·5 mm). The results are given in Table 4 in the form of an analysis of variance. It will be seen that the variance between individuals on the same panel is, as would be expected, significantly less than the variance between individuals taken from panels which were mounted in different positions on the board and carried different population densities. Nevertheless, the variation in weight on a single panel is considerable, the mean square

corresponding to a standard deviation of 0·21 g or 38% of the mean weight. The variance showed some increase with the mean, so a logarithmic transformation might have slightly improved the efficiency of the analysis, but this was not considered worth while over the range of observations made. Individual differences became apparent quite early in growth. While some faster-growing individuals persisted so throughout the season, others slowed down to be overtaken by smaller individuals. There was some advantage in early settlement and most of the larger spat maintained this advantage until the middle of June, by which time they had reached 5-7 mm in diameter. Thereafter the initial order of sizes was not maintained, so that by the end of the experiment the order of increasing weight bore only a slight resemblance to the initial order of increasing size.

The variation between panels is further analysed in Table 5 into the effect of the four positions A, B, C and D on the board, and the effect of population density. Both variances exceeded that between individuals on a single panel, but only the

Table 5. *Analysis of variance of differences between panels*

Source of variation	Degrees of freedom	Sum of squares	Mean square	Variance ratio
Between positions A, B, C and D	3	10·6291	3·5430	6·23
Between population densities	2	2·6541	1·3271	2·35
Interaction	6	3·4056	0·5676	1·00
Total	11	16·6888	–	–

Mean values: A 0·582 g; B 0·661 g; C 0·588 g; D 0·416 g — 0·609 g (Differs significantly from A, B and C)

4/cm² 0·530 g (For A, B and C only 0·573 g)
1/cm² 0·613 g (For A, B and C only 0·665 g)
0·25/cm² 0·650 g (For A, B and C only 0·734 g)

differences between positions were significantly greater than the interaction variance at the 5% level of probability.

INFLUENCE OF CURRENT FLOW

Sessile organisms generally reach their greatest size when growing in estuaries or channels with fast-flowing streams or on headlands exposed to swell, strong currents, or both (Crisp 1955). The advantage to barnacles of a site with a current over a more stagnant one was shown by Moore (1936) and by Hatton (1938), but since their comparisons were made between different places it is possible that the content of suspended matter carried in the water was different also. In the comparisons described here the barnacles growing on surfaces A, B and C on the one hand, and those growing on D on the other, were placed in the same flow of water. Their environment was therefore identical in every respect other than the restriction of water flow by the baffles placed vertically between the panels on surface D. Table 5 includes the mean weights of barnacles on each of the four surfaces and shows that the significance of the effect of position (see above) is mainly due to the small size of barnacles on surface D. Furthermore, the barnacles growing on

the margins of panels mounted between baffles were smaller than those growing in the centre of the panel, especially those on the downstream side of the baffle plate. This is to be explained by the fact that the water at the margins adjacent to the

Table 6. *Mean weights of individuals at centre and at margins of panels*

	Mean weight (g) of barnacles situated: at margins	at centre
Normal panels: 2, 9 and 6	0·870	0·732
Panels with baffles: 3, 7 and 12	0·350	0·405
Margin behind baffles	0·296	–
Margin in front of baffles	0·373	–

baffle plates would be more stagnant than water passing over the centre of the panel. On the panels mounted normally without baffle plates no such difference was observed, those at the margins being in fact larger than those in the centre

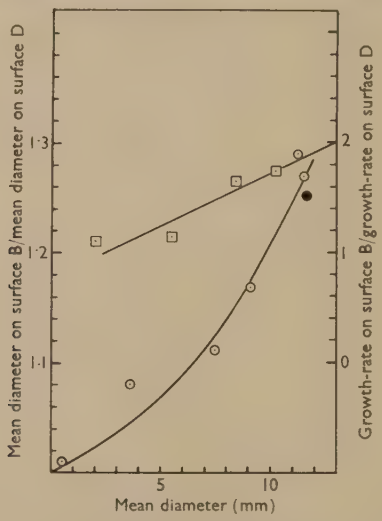


Fig. 2. Comparison of the growth of barnacles on surface B exposed to the current and on surface D protected by baffles: —⊙—, ratio of diameters; the black circle was calculated from the cube root of the final mean weights: —⊡—, ratio of growth-rates. In each case the ratio, expressed as the mean value for barnacles on surface B divided by the mean value for surface D, is plotted against the mean diameter of both sets of barnacles.

(Table 6). Evidently quite small differences in the rate of circulation of water over the barnacle is sufficient to influence its rate of growth.

These differences were analysed further by measuring the rostro-carinal diameters of a number of individuals growing on the panels mounted between baffles on surface D and on a similar number of panels mounted normally on surface B. The

size of barnacles exposed directly to the current was not at first very different from the size of those growing on the sheltered panels, as can be seen from the ratio of their mean diameters shown by the lower line in Fig. 2. As growth proceeded, the difference between the two sets became more obvious, and by the time the mean size reached about 12 mm the mean diameter of the individuals on surface B exceeded those on surface D by nearly 25%. This figure agreed well with the cube root of the ratio of their mean weights, thus proving that the diameter gave a reasonably accurate indication of growth. The upper line in Fig. 2 shows the ratio of the mean growth-rates of the two groups; it can be seen that as the barnacles increased in size, the difference in growth-rate between the two groups also increased. The advantage held by the individuals growing in a current became progressively greater as they grew larger in size. This observation may be related to two factors which alter during growth. First, younger specimens have a faster cirral beat and appear to depend less on holding the cirri extended against the water current to gather their food; the current may, therefore, confer less benefit to younger individuals. Secondly, when water flows over a surface, it experiences drag, so that the water close to the surface flows more slowly than the water further away (for discussion see Crisp 1955). A barnacle in a current, as it grows, is able, therefore, to reach water which, being further removed from the surface, is moving faster. Thus the amount of food carried by the current to unit area of the cirral net increases during growth, whereas no such progressive benefit falls to a barnacle feeding by its own effort in still water.

INFLUENCE OF PITS

In view of the importance of water flow, it was thought desirable to investigate whether the shelter afforded by the small pits into which the barnacles first settled had any influence on their early growth in the way that Hatton (1938) has described. These pits were slightly deeper than the height of the just metamorphosed barnacle, but its cirri could protrude from the pit. Nevertheless, such a barnacle would feed in slower-moving water than one settled on the surface of the panel. Four panels were exposed in 1955 at a time when the cyprids were sufficiently abundant to settle both in the pits and on the surrounding plane surface. Near-by pairs were selected, one in a pit and one on the surface, and others removed. The panels were photographed in the usual way and the growth-rates compared after the lapse of 15 and 32 days. The results from forty such pairs distributed over the four panels are given in Table 7. The pits have a small and barely significant effect on growth during the first 15 days, but this is overshadowed by the subsequent growth of the barnacle beyond 5 mm. The result is comparable with Hatton's observations, which showed a more pronounced and prolonged effect. The growth-rates and presumably the food content of the water at St Malo were much smaller. Under these less favourable conditions, the effect of a poor start in growth might be more sustained. Moreover, the natural pits in the rock studied by Hatton were probably more variable and deeper than the artificial pits used in my experiments.

INFLUENCE OF ORIENTATION ON GROWTH-RATE

Several authors have assumed that a barnacle would be able to feed more efficiently if its rostral compartment were oriented towards the current source and, in consequence, the concave surface of its cirral net normally faced the flow of water (Moore 1935, Crisp 1953, 1955, Crisp & Stubbings 1957). The assumption seemed reasonable because many species feed by holding the cirral net extended against the current (Crisp 1950, Crisp & Southward 1956, Southward & Crisp 1959), and furthermore the whole shell rotates during growth in many species bringing the cirral net to face the predominant flow of water over the barnacle (Crisp 1953, Crisp & Stubbings 1957). This rotation has been regarded as probably adaptive, allowing the barnacle to feed with the least expenditure of energy.

As an initial test of the influence of orientation on growth, the panels on surfaces A, B and C only were grouped according to the direction of the orientation of the majority of barnacles present in relation to the assumed direction of water flow

Table 7. *Influence of pits on early growth*

Panel and condition	Mean diameter (mm)			Difference in growth of individuals on plane surface—that of individuals in pits (mm)	
	Start	15 days	32 days	0-15 days	15-32 days
No. 1 Plane surface	1·45	2·98	4·17	0	−0·06
No. 1 Pits	1·65	3·18	4·43		
No. 6 Plane surface	1·24	2·50	5·41	+0·07	−0·24
No. 6 Pits	1·25	2·44	5·59		
No. 8 Plane surface	1·21	2·56	6·33	+0·40	+0·16
No. 8 Pits	1·29	2·24	5·85		
No. 11 Plane surface	1·20	2·53	5·79	+0·34	−0·03
No. 11 Pits	1·25	2·24	5·53		
Mean plane surface	1·27	2·64	5·43	+0·20	−0·04
Mean Pits	1·36	2·53	5·35		

over the board on which they had been mounted. As will be seen from Table 2, the resulting groups of panels, viz. 4, 6 and 11; 5, 9 and 1; and 10, 2 and 8, were balanced in respect of density groupings, position on the board, and position order from the leading edge of the board α, β and γ. Inevitably the numbers present on the different panels varied, so that the mean of the average weight of barnacles on each of the three panels (called the unweighted mean) was not identical with the mean weight of all the barnacles on all three panels (called the weighted mean). From Table 8 it can be seen that the unweighted means show a gradation in size in relation to orientation in the expected sense. The weighted means, however, do not bear this out so clearly. Moreover, an analysis of variance showed that the variations due to orientation were not significant in relation to the random differences between panels, as given by the interaction term in Table 5. The failure to obtain a significant effect might, therefore, have been due to large inter-panel differences and also to the fact that by no means all the barnacles on each panel were similarly oriented. Both these objections were

overcome by the more laborious procedure of ascertaining the weight and orientation of each individual, and dividing the individuals on each panel into three orientation groups. For this purpose panels or parts of panels were selected which bore barnacles belonging to at least two orientation groups. A revised analysis was carried out, the results of which are included at the foot of Table 8. It will be seen that the differences due to orientation, which were particularly clearly shown by the unweighted means, were confirmed. The variance due to orientation was

Table 8. *Influence of orientation on growth*

Mean weight (g) reached by 21 November 1954

Orientation	Unweighted means		Weighted means	
	Classified by panels	Classified by individuals	Classified by panels	Classified by individuals
Carinal end towards current source	0·591	0·565	0·600	0·577
Rostro-carinal axis at right angles to current	0·648	0·632	0·571	0·593
Rostral end towards current source	0·732	0·701	0·649	0·646

ANALYSIS OF VARIANCE

Source of variation	Degrees of freedom	Sum of squares	Mean square
Between panels	10	6·9464	0·6946
Between orientations	2	0·8264	0·4132
Interaction	18	1·3092	0·0727
Between individuals	997	41·5928	0·0417
Total	1027	50·6748	

significant both in relation to the individual variance and the interaction term. The influence of orientation, however, was not large; from the data in Table 8 a favourable orientation appears to confer an advantage amounting to an increase of weight of about 10% or 3% by linear measurement. The small magnitude of the difference in linear growth-rates produced by differences in orientation was confirmed from measurements on young individuals made in the spring of 1955.

Table 9. *Growth-rates of small individuals in relation to orientation*

Orientation	Mean diameter (mm) after:			Mean rate of growth (mm/day)
	0 days	15 days	32 days	
Rostral end towards current source (+)	1·35	2·75	5·33	$1·25 \times 10^{-2}$
At right angles to current (~)	1·29	2·44	4·94	$1·14 \times 10^{-2}$
Carinal end to current source (−)	1·34	2·68	5·09	$1·17 \times 10^{-2}$

Table 9 summarizes the mean diameters and rates of growth of some seventy small barnacles at their period of maximum linear growth. The results are of the same order as those analysed above, and are consistent with orientation having a small but definite part in determining rate of growth. The small order of the effect produced by orientation is doubtless due to the ability of the barnacle to correct for a wrong orientation by twisting the cirral net to bring its surface against the flow of water by means of the muscles of the prosoma.

INFLUENCE OF POPULATION DENSITY ON GROWTH

The analysis of variance given in Table 5 shows that, although barnacle weight decreased as the population density increased, the effect was not quite significant in relation to the large interaction term. A further analysis was therefore conducted, analogous to that described in the previous section, which took advantage of the fact that the population density was not uniform throughout each panel. The weights of barnacles growing at the edges of each panel, or adjacent to spaces where neighbouring individuals had accidentally been lost, were compared with the weights of other barnacles on the same panel growing at a population density greater than that of the majority, for example where two individuals instead of one had grown in a single pit. In this way differences between panels were eliminated, and the differences due to population density, although based on fewer measurements, were highly significant in comparison with the residual. In this case the interaction variance (density × panels) was smaller than the variance between individuals and the two were therefore grouped together (Table 10). Further, the average weight of barnacles was calculated within areas where the

Table 10. *Comparison of weights of 196 barnacles from densely and sparsely populated areas on a panel*

Mean weight from densely populated areas —0·576 g
Mean weight from sparsely populated areas—0·642 g

ANALYSIS OF VARIANCE

Source of variation	Degrees of freedom	Sum of squares	Mean square
Between panels	11	5·2725	0·479
Between dense and sparse areas	1	0·2087	0·209
Residual	183	9·2712	0·051
Total	195	14·7525	

barnacles were more closely, or more sparsely, packed than on the remainder of the panel, and the population density of each area was measured within a radius of 1·5 cm. These measurements were used to widen the range of population density over which its influence upon the mean weight was investigated. The result is shown in the middle curve of Fig. 3*a*. The regression line shown, though not entirely reliable because of the extent of individual variation, shows quite clearly that the differences in weight caused by changes in population density are rather small. The mean weight of individuals which have ample space in which to grow does not exceed twice that of crowded individuals having initially only 0·25 cm^2 each. This is a remarkably small difference in weight, when it is borne in mind that the area occupied by freely growing barnacles exceeds 2·0 cm^2. The crowded specimens make good by growth in height much of the volume which they would lose on account of their smaller basal area.

In Fig. 3*b* the mean values of the maximum diameter are plotted against time, for the barnacles on the three panels on surface B having population densities of 0·25, 1·0 and 4·0 individuals per cm^2 respectively. During the initial period the close similarity in rates of growth is evident, for the curves diverge appreciably

only after the barnacles touch each other, that is at the point marked P_2 for panel 2 and P_6 for panel 6. The similarity in growth-rates over a wide range of population density can be seen from the upper curve of Fig. 3*a*. This gives the values of the initial rate of growth between 2 and 8 mm in diameter, which is approximately linear with respect to time, as a function of the population density. The fall in the growth-rate for population densities exceeding 2·0 individuals per cm² was due to some of the barnacles having come into contact before reaching 8 mm. In further experiments carried out in 1955 on very young barnacles the growth curve of individuals settled in groups having a population density as high as 10/cm² was, up to the time that they came into contact with each other, indistinguishable from that of isolated individuals or from the results obtained in 1954.

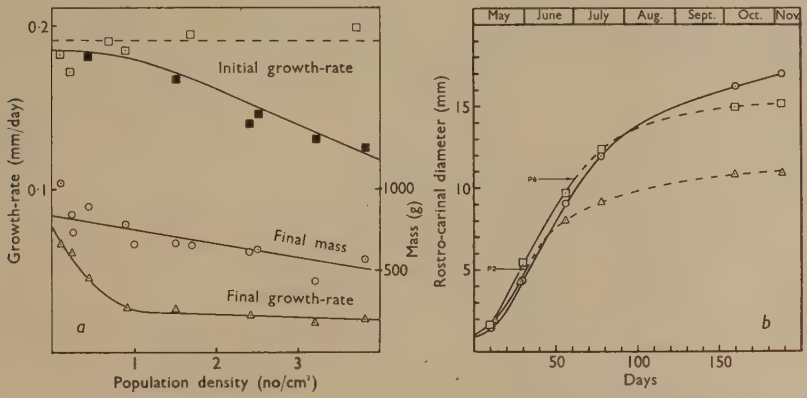


Fig. 3. *a*, The relation between population density and rates of growth. Upper curves, initial linear growth-rate of rostro-carinal diameter: ⊡ isolated individuals (broken line), ■ individuals in contact with others (full line); middle curve, mean weight at end of experiment; lower curve, final linear growth-rate of rostro-carinal diameter.

b, Growth in relation to time at three population densities (panels 2, 6 and 9). P_2 and P_6 indicate the approximate point at which the individuals came into contact with one another on panels 2 and 6 respectively and the subsequent growth of these individuals is shown by a broken line.

After this period of initial growth, the barnacles come into contact, and as will be seen from Fig. 3*b* the rate of increase in diameter falls off. The barnacles continue to grow, however, even after they have occupied all the space originally allocated to them. For example, on Panel 2 the barnacles were initially 0·5 cm apart and so touched when their mean diameter was 5 mm; further growth enabled them to fill up the remaining spaces. Thus the maximum diameter of the barnacles measured along the diagonals of the square lattice formed by their centres could reach a value of $0{\cdot}5 \times \sqrt{2} = 7{\cdot}1$ mm. The graph shows, however, that their mean diameter increased to at least 10 mm. This anomaly was caused by the pressure in the plane of the panel surface exerted by the growing barnacles which forced the marginal individuals outwards, often right over the side of the panel, so making room for the continued expansion of the more central ones. This force, as Barnes

& Powell have described (1950), is capable of lifting groups of barnacles off the substratum if they cannot expand outwards.

The bottom curve in Fig. 3*a* shows the rate of growth during the period 2 August to 21 November 1954, as a function of population density. Free space was available to individuals growing at densities of less than 1 individual per cm², and their growth-rate was correspondingly higher than that of more crowded individuals. The latter grew slowly and their rate of growth against the lateral pressure to which they were exposed was not very dependent on population density, falling from 0·05 to 0·03 mm per day with an increase in the initial density of from 1·0 to 5·0 individuals per cm².

The decrease in growth-rate with increasing density of population as measured by the mean final weight (Fig. 3*a* middle curve), might have been the result of (*a*) mutual interference between contiguous individuals from such causes as growth with the shells under mutual pressure, or contact between two or more cirral nets, or (*b*) to simple competition for the available food, or (*c*) to both effects. In order to distinguish between these possibilities, a series of comparisons were made between

Table 11. *Comparison of growth-rates of pairs of individuals in a pit and of single individuals at the same average population density*

Average density of population on panel (no./cm²)	Ratio of mean linear growth-rate: doublets/singletons			Ratio of final mean weights
	26 May–15 June	26 May–10 July	20 August–21 September	
0·25	0·97	1·08	0·82*	0·98
1·00	1·00	1·02	0·65*	0·99
4·00	0·70*	0·82*	0·69*	0·76

* Linear growth of paired individuals restricted by lack of space.

the growth-rates of individuals growing singly, and of others which had by chance settled as a pair in a single pit. These latter individuals were growing in contact from the outset, and could interfere with each other, but they were surrounded by a population density which was nearly the same as that surrounding single individuals. The growth-rates of about seventy such pairs were measured and also those of the same number of singletons near by. Table 11 gives the ratio of the growth-rates of contiguous individuals divided by that of the single ones. The comparison indicates that close proximity of itself did not influence growth-rate, whether measured as rate of expansion of the barnacle's diameter or as its final weight. When, later in the season, the space became very restricted, individuals growing in pairs could not expand in area as well as single ones. However, up to a density of 1·0 individual per cm², this did not influence the final weight which they reached. In the very dense group, however, both diameter increase and final weight were less in barnacles growing in pairs, presumably because at a density of 4·0 individuals per cm² the presence of an additional individual critically influenced the amount of food available in the immediate neighbourhood.

The effect of the pressure of growth of a crowded population of *Balanus balanoides* on another species, *Elminius modestus*, was illuminating. The mean growth curves for the occasional specimens of *Elminius* found to have settled in the population predominantly of *Balanus balanoides* are shown in Fig. 4. The initial growth of *Elminius*, like that of *Balanus*, is not dependent on the density of barnacles among which it is growing. When the specimens of *Balanus* reach a sufficient size, however, they squeeze the *Elminius*. In a population of density 1·0 individual per cm^2 *Elminius* ceased to expand after reaching 7-8 mm, and in a population of 4·0 individuals per cm^2 it is actually squeezed into a smaller area after attaining a diameter of 7·0 mm.

INFLUENCE OF POSITION ON PANEL

In a population of barnacles growing in a unidirectional current, those growing

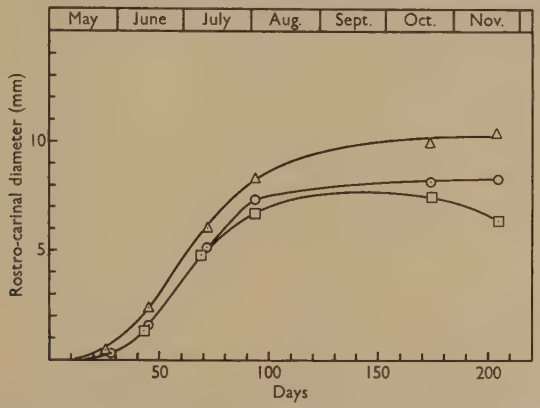


Fig. 4. Growth-rate of specimens of *Elminius modestus* growing among populations of *Balanus balanoides*. Three population densities: —△— 0·25 *B. balanoides* per cm^2; —⊙— 1·0 *B. balanoides* per cm^2; —⊡— 4·0 *B. balanoides* per cm^2.

on the side towards the source of the current will have the first opportunity to collect food particles. They would be expected to grow more rapidly than those behind them, since the latter collect from a stream of water which carries an ever-decreasing load of nutrient particles, provided that the water flows over the barnacle-covered surface as a series of laminar layers. The mean weight of barnacles near the leading edge of each panel was therefore compared with that of barnacles in the centre and at the trailing edge. From the results shown in Table 12 it will be seen that the position of the barnacle relative to the leading edge of the panel had little influence on its rate of growth. In certain panels the first and last rows of barnacles were distinctly smaller than those distributed over the rest of the surface, this being probably due to their having grown over the edge and so become directed away from the freely flowing water. Apart from these, there was little evidence indeed that barnacles at the front were larger than those at the rear end of the panels.

Growth-rates of other species

Occasional specimens of *E. modestus* and of *Balanus crenatus* were found to have settled among *B. balanoides*. The mean growth-rates of freely growing specimens of these two species, together with that of *B. balanoides* are shown in Fig. 5. The growth curve for *B. crenatus* was steeper than that of *B. balanoides*, as previously shown by Barnes & Powell (1953), and its growth terminated more abruptly in the autumn. The linear growth-rate of *Elminius modestus* was almost equal to that of *Balanus balanoides*, but its limiting size of about 10 mm was reached sooner. These three species differed in the time at which they reach maturity. *Elminius modestus*, the smallest species, reaches maturity at approximately 5 mm diameter and breeds at any time of year. *Balanus balanoides* and *B. crenatus* breed at a particular season of the year, the former in November and the latter between January and July and sometimes later. In their first year therefore *B. balanoides*

Table 12. *Mean weight of barnacles at front and rear end of panels*

Only panels bearing a density of 4 and 1 barnacle per cm² contained sufficient individuals for a comparison to be made.

Row	Density 4/cm² (Panels 1, 2 and 4)		Density 1/cm² (Panels 5, 6 and 8)	
	Mean weight (g)	No. of barnacles contributing to mean	Mean weight (g)	No. of barnacles contributing to mean
1st at front end	0·682	35	0·632	26
2nd from front end	0·605	36	0·710	28
3rd from front end	0·749	42	0·707	22
4th from front end	0·641	37	0·643	33
Rows in centre of panel	0·547	84	0·704	36
4th from rear end	0·620	34	0·740	30
3rd from rear end	0·632	35	0·638	31
2nd from rear end	0·531	32	0·624	26
Last at rear end	0·444	33	0·607	27

and *B. crenatus* grown under favourable conditions on a raft passed the critical size at which they could bear eggs and possessed a well-formed ovary several months before the eggs were fertilized. First-year *B. balanoides* did not become fertilized under raft conditions until late November, and first-year *B. crenatus* not until mid-January. All three species showed the same general form of growth. At first, just after metamorphosis, the rate of growth of the rostro-carinal diameter accelerated, then became steady, and finally slowed down. The deceleration of growth set in roughly at the stage when the gonads were beginning to develop in all three species. Individuals of all three species grew to a larger size on the raft than on typical areas of shore or sub-littoral rock. However, groups of individuals found growing intertidally on structures exposed to very strong currents, such as on the sides of the supports of the Telford Suspension Bridge, or in channels of a narrow section of the Menai Straits known as the Swillies, reached sizes comparable with those reached on the raft.

THE INFLUENCE OF ENVIRONMENTAL FACTORS

In spite of the differences between the two localities, especially in regard to the turbidity of the water, the results obtained for the rates of growth under raft conditions of *B. balanoides* and *B. crenatus* by Barnes & Powell (1953) in the Clyde, and those recorded here from the Menai Straits are closely similar to each other. This similarity, together with the high order of magnitude of the growth-rates, suggests that the conditions of exposure on a raft in a tideway may be optimal for such barnacles; certainly the conditions are far better from the point of view of growth than those which obtain on a typical rocky shore.

Nevertheless, not all the individuals grew at the same rapid rate, and differences could readily be detected even between adjacent specimens, where the local

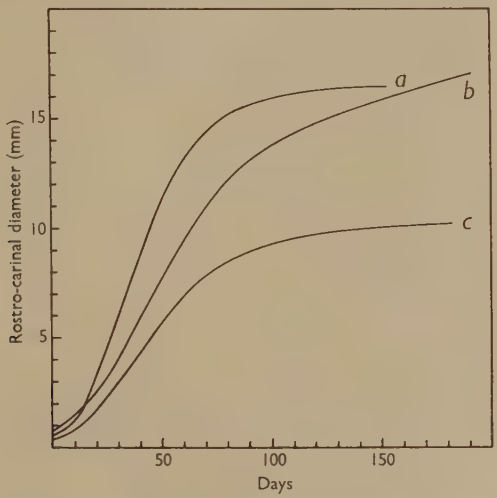


Fig. 5. Growth curves, adjusted to the same starting point, for *Balanus crenatus* (*a*), *B. balanoides* (*b*) and *Elminius modestus* (*c*).

environment would have been expected to be identical. The coefficient of variation in weight, within the compass of a single panel, was as high as 30-40%. Another such difference was the variability in the time of appearance of marginal crenations and ridges around the base. The photograph taken on 10 July (Plate 3) shows these differences particularly clearly. These individual variations, whether they are of a genetic type or due to unsuspected differences in environment, emphasize that the effects discussed below relate only to what can be observed in a population. A particular individual may well show variations outside the range of difference produced by the experimental treatments used.

Of the differences produced by the artificial treatments, the most profound was that caused by restricting the free flow of water over the panels, which reduced the mean growth-rate to about that of individuals growing at low water in a good intertidal habitat near by. Hence the high growth-rates observed on a raft, and on

similar habitats such as pier piles in deep water, can be attributed to the frequent exchange of water past the barnacle. As a rider on the principle that a rapid flow of water benefits the barnacle, it follows that individuals settled in pits are at a disadvantage, as has in fact been shown. Conversely those settled on prominences being in a faster-flowing layer of water grow more rapidly.

The density of the population ranked next in importance in determining the mean growth-rate. However, the reduction in growth-rate with increasing population density was not as great as would have been expected on the basis of competition for a limited quantity of suspended food. If the total amount of food available per unit area of panel surface were constant, an increase in density from 1 to 5 individuals per cm^2 would result in a corresponding decrease in mean weight from 850 to 170 g. In fact, the mean weight fell only to about 470 g (Fig. 3*a*). Therefore the fivefold increase in numbers resulted in an increase of two and a half fold in the amount of food collected. From this it follows that the food available under the conditions prevailing during the experiment was sufficient, at the lower population densities, to support a faster rate of growth, had the barnacles been capable of gathering it. The greater collecting rate of the more closely packed population may be accounted for by the fact that the cirral net is not normally extended by a barnacle for the whole of the time, since it must be withdrawn for the transfer of particles to the smaller cirri and mouth parts. The more food particles there are in suspension, the more frequently must these withdrawal movements be made, so that, during the time that one barnacle has withdrawn its cirri, an adjacent one is able to collect food without causing hardship to its neighbour. This would not be so if the food particles were more sparse, for then all the individuals would spend most of the time with their cirri hopefully extended, and would collect all or the greater number of the particles available. They would therefore compete more stringently with one another. This latter picture may represent more closely the situation at open coast stations, such as Port Erin, where the growth-rate is generally smaller, and where, according to Moore, the competition between neighbouring individuals is more in evidence. It is surprising that under raft conditions competition appeared to play so small a part in determining growth-rate. Particularly remarkable was the fact that the leading rows of barnacles, which had the first opportunity to collect from the water passing horizontally over the panel, showed little evidence of reaching a larger size than those behind them. Probably the uneven contour produced by the surface of the barnacles and their waving cirri caused turbulent flow, thereby increasing the exchange of water normal to the surface. If this exchange were large enough and if food were sufficiently plentiful, each barnacle could feed without seriously competing with its neighbour.

The influence of orientation on growth was rather small, and therefore more difficult to demonstrate. Since individuals placed with the rostral compartment towards the current source did, in fact, reach a slightly larger size and so produced more offspring, it follows that the ability to settle in or rotate towards this position would confer an advantage and be of adaptive value.

The only other factor demonstrated, the effect of harbouring the parasite *Hemioniscus balani*, differed from the others in being accidentally acquired. In consequence, it did not form part of a planned experiment and such conclusions as could be drawn had to be based on fewer observations than was desirable. The reduction in the growth-rate was considerable, and more than was expected in relation to the size of the parasite.

The effect of all the above factors, apart from the last, can be interpreted qualitatively as being the result of expected differences in the rate of collection of food. The same is true of the influence of tidal level demonstrated by Barnes & Powell (1953), though in this case a quantitative measure can be applied. If the initial value of specific growth-rate quoted by these authors is divided by the

Table 13. *Growth-rate in relation to time of submergence (Data from Barnes & Powell* 1953)

Barnacle group	Specific initial growth-rate, r	Fraction of time submerged, f	Specific initial growth-rate per 24 h submergence time
II	1·5	0·25	6·00
III	2·9	0·42	6·90
IV	3·7	0·57	6·50
V	4·0	0·73	5·50
VI	4·45	0·90	4·95
VII	4·3	1·00	4·30
Raft	5·45	1·00	5·45

proportionate time of immersion, the rate of growth for a unit feeding time of one day is obtained (Table 13). It can be seen that this rate, while more constant than the actual growth-rates, increases at higher tidal levels. Such an effect is not unexpected, since barnacles near high water mark will be affected beneficially by wave action for the greater part of the time they are submerged, while those at low water mark will spend the greater part of the time in water which is quiet and less beneficial for growth.

THE GROWTH CURVE

Most of the factors influencing growth appear to do so by influencing the rate of collection of food particles. It is therefore worth considering how far the form of the growth curve itself reflects the ability of the barnacle to obtain food. Let us consider a barnacle of volume v growing isometrically. Any linear dimension l will be related to volume as $v = k_1 l^3$, and to the area a of the cirral net as $a = k_2 l^2$. If the barnacle is feeding in a stream of uniform velocity u, containing n particles per unit volume, its feeding rate f, assuming it utilizes all available particles, will be: $f = nua = k_2 nul^2$. Its rate of increase in volume may be supposed to be proportional to f through a factor e representing the efficiency of the transformation of food into barnacle tissue.

$$\text{Then} \quad \frac{dv}{dt} = ef = k_2 enul^2$$

$$\text{Since} \quad \frac{dv}{dt} = 3k_1 l^2 \frac{dl}{dt},$$

$$\text{and} \quad \frac{dl}{dt} = \frac{k_2}{3k_1} enu = \text{constant}.$$

Thus a barnacle growing in a steady current of water, where food collection alone is limiting, would be expected to show uniform linear growth. This is indeed approximately true of the middle period of growth. Hence the rate of increase in diameter of the barnacle seems preferable to the concept of 'specific growth-rate' employed by Barnes & Powell as an index of growth. In the first place, it can be more conveniently and accurately measured, since it remains sensibly constant for a large part of the animal's life. In the second place, the constancy of the rate of growth so defined may be regarded as a natural result of the animal's mode of feeding and it may prove possible to relate its magnitude to the shape and metabolic efficiency of the animal, and to the nutrient content of the water in which it lives. The specific growth-rate, l^{-1}. $dl\ dt$, on the other hand, since it may also be written $d(\log_e l)\ dt$ carries the suggestion of logarithmic increase in size, which is hardly justifiable.

The non-linear part of the sigmoid growth curve consists of an acceleration of growth just after metamorphosis and a deceleration after maturity is reached. The first may be explained as follows. The sharp velocity gradient of water flow near the solid surface on which the barnacles are growing will cause the flow-rate of water past the cirri to increase initially with the first power of the dimensions of the barnacle. Calling this rate of flow V, and assuming $V = g(l)$, the relation for maximum growth-rate corresponding to the first equation becomes:

$$\frac{dl}{dt} = \frac{k_2}{3k_1} g(l)$$

and hence increases as l increases.

If we assume instead that at this early stage feeding depends mainly upon active capture by the cirral net, a similar conclusion is reached. The volume swept out will be roughly proportional to l^3, say $k_3 l^3$ where k_3 is proportional to rate of beat and swept-out volume at each beat. Hence:

$$f = k_3 enl^3 \quad \text{and}$$

$$\frac{dl}{dt} = \frac{k_3}{3k_1} enl$$

The rate of growth again appears to accelerate with increasing size, though k_3 is probably not constant but falls, since the beating rate usually decreases with growth.

After maturity, growth slows down. This can have little to do with nutrition,

for it happens independently of changes in the food supply. Thus the growth of *Elminius*, after it reaches a diameter of 6-7 mm, slows down whatever the season of year. Species, such as *Balanus crenatus* (Barnes & Powell 1953), *B. balanoides* (Runnström 1925, Hatton 1938) and *B. balanus* (= *B. porcatus*) (Crisp 1954, Barnes & Barnes 1954), which take longer to reach maturity, show renewed growth in their second and third seasons if, for any reason, they have not passed through the linear phase of growth at the time that unfavourable environmental conditions interrupt it. The slowing down in growth-rate is therefore caused primarily by metabolic changes in the animal, which occur after the onset of maturity, though seasonal environmental effects may be superimposed on the ideal form of the growth curve.

SUMMARY

1. A method of producing a pre-arranged pattern and density of barnacle settlement is described, which makes use of the tendency for barnacle cyprids to settle in small pits. The pits had a negligible influence on growth-rate after the first 2 weeks. This method was used to study the influence of water flow, population density and orientation on the rate of growth of *B. balanoides* in the Menai Straits, North Wales.

2. Barnacles parasitized by *Hemioniscus balani* grew more slowly than unparasitized individuals.

3. The passage of an uninterrupted current of water over the barnacles was the most important factor in promoting rapid growth.

4. Population density appreciably influenced growth in volume only when the individuals were closely packed, either touching or nearly touching. Even at densities as high as 4 individuals per cm^2, much of the loss in cross-sectional area caused by space limitation was compensated for by increase in height. The effect of close packing in itself did not appear to be harmful.

5. In a unidirectional current, there was little evidence that the leading individuals in a group grew appreciably faster than the trailing ones.

6. Orientation with the rostrum pointing to the current source conferred an advantage resulting in slightly enhanced growth.

7. It is shown that a barnacle whose growth is isometric and determined only by the rate of intake of food from a current of constant nutrient content would grow at a constant linear rate. This is approximately true for the greater part of the growth curve of the species investigated. Early growth just after metamorphosis is slower, probably because the rate of water flow is reduced in the immediate vicinity of the solid substratum. Growth slows down after maturity in all species as a consequence of metabolic changes.

REFERENCES

Barnes, H. (1953). The effect of light on the growth rate of two barnacles *Balanus balanoides* (L.) and *B. crenatus* Brug. under conditions of total submergence. *Oikos*, **4**, 104-11.

Barnes, H. (1955). The growth rate of *Balanus balanoides* (L.). *Oikos*, **6**, 109-13.

Barnes, H. & Barnes, M. (1954). The general biology of *Balanus balanus* (L.) da Costa. *Oikos*, **5**, 63-76.

Barnes, H., Crisp, D. J. & Powell, H. T. (**1951**). Observations on the orientation of some species of barnacles. *J. Anim. Ecol.* **20,** 227-41.

Barnes, H. & Powell, H. T. (**1950**). The development, general morphology and subsequent elimination of barnacle populations, *Balanus crenatus* and *B. balanoides*, after a heavy initial settlement. *J. Anim. Ecol.* **19,** 175-9.

Barnes, H. & Powell, H. T. (**1953**). The growth of *Balanus balanoides* (L.) and *B. crenatus* under varying conditions of submersion. *J. Mar. Biol. Ass. U.K.* **32,** 107-28.

Corlett, J. (**1948**). Rates of settlement and growth of the 'pile' fauna of the Mersey estuary. *Proc. Lpool. Biol. Soc.* **56,** 2-28.

Crisp, D. J. (**1950**). The breeding and distribution of *Chthamalus stellatus*. *Nature, Lond.* **165,** 409.

Crisp, D. J. (**1953**). Changes in the orientation of barnacles of certain species in relation to water currents. *J. Anim. Ecol.* **22,** 331-43.

Crisp, D. J. (**1954**). The breeding of *Balanus porcatus* (da Costa) in the Irish Sea. *J. Mar. Biol. Ass. U.K.* **33,** 473-96.

Crisp, D. J. (**1955**). The behaviour of barnacle cyprids in relation to water movement over a surface. *J. Exp. Biol.* **32,** 569-90.

Crisp, D. J. & Barnes, H. (**1954**). The orientation and distribution of barnacles at settlement with particular reference to surface contour. *J. Anim. Ecol.* **23,** 142-62.

Crisp, D. J. & Southward, A. J. (**1956**). Demonstration of small scale water currents by means of milk. *Nature, Lond.* **178,** 1076.

Crisp, D. J. & Stubbings, H. G. (**1957**). The orientation of barnacles to water currents. *J. Anim. Ecol.* **26,** 179-96.

Hatton, H. (**1938**). Essais de bionomie explicative sur quelques espèces intercotidales. *Ann. Inst. océanogr. Monaco* (N.S.), **17,** 241-348.

Hatton, H. & Fischer-Piette, E. (**1932**). Observations et expériences sur le peuplement des côtes rocheuses par les Cirripèdes. *Bull. Inst. océanogr. Monaco,* No. 592.

Klugh, A. B. & Newcombe, C. L. (**1935**). Light as a controlling factor in the growth of *Balanus balanoides*. *Canad. J. Res.* **13** (D), 39-44.

Moore, H. B. (**1934**). The biology of *Balanus balanoides*. I. Growth rate and its relation to size, season and tidal level. *J. Mar. Biol. Ass. U.K.* **19,** 851-68.

Moore, H. B. (**1935**). The biology of *Balanus balanoides*. IV. Relation to environmental factors. *J. Mar. Biol. Ass. U.K.* **20,** 279-307.

Moore, H. B. (**1936**). The biology of *Balanus balanoides*. V. Distribution in the Plymouth area. *J. Mar. Biol. Ass. U.K.* **20,** 701-16.

Moore, H. B. (**1958**). *Marine Ecology*. New York.

Runnström, S. (**1925**). Zur Biologie und Entwicklung von *Balanus balanoides* Linné. *Bergens Mus. Aarb.* Nr. 5.

Southward, A. J. & Crisp, D. J. (**1959**). Modes of cirral activity in barnacles. *Proc. XV Int. Congr. Zool.* 1958, 295-6.

Topsent, E. (**1911**). Croissance et mort des balanes à Luc sur Mer. *Ann. Inst. océanogr. Monaco,* **2,** fasc. 6.

THE DISTRIBUTION OF *NEPHTYS CIRROSA* AND *N. HOMBERGI* ON THE SOUTH-WESTERN COASTS OF ENGLAND AND WALES

By R. B. CLARK and E. C. HADERLIE*

Department of Zoology, University of Bristol

(With 7 Figures in the Text)

Members of the polychaete family Nephtyidae are commonly found in both sublittoral and intertidal deposits of sand and mud in most parts of the world. Only two species of *Nephtys*, *N. hombergi* Lamarck and *N. cirrosa* Ehlers, are common around the south and west coasts of Britain and, at least in the intertidal zone, these two very similar worms appear to occupy distinct and separate habitats. *N. hombergi* occurs in the mouths of estuaries (Allen & Todd 1900, 1902; Bassindale 1938; Spooner & Moore 1940; Holme 1949) and lives in finer deposits than *N. cirrosa*, which is usually found only in clean sand on the open coast. A comparable ecological separation of the local species of *Nephtys* has been reported from other parts of the world. Thus, in New England, *N. picta* Ehlers occurs in muddy sand and *N. bucera* Ehlers in clean, shifting sand (M. H. Pettibone, *in litt.*) and on the Pacific coast of north America, another pair of species, *N. caecoides* Hartman and *N. californiensis* Hartman, occupy these two distinct habitats (Hartman 1950, 1954). The ecological isolation of each member of a pair of species from the other appears to be almost complete and it is not usual to find more than one species on any beach.

In this investigation we have tried to give greater precision to these statements of the ecological preferences of the worms as a step towards defining the optimal and tolerable habitats of different species of *Nephtys*. This paper concerns *N. cirrosa* and *N. hombergi*; the two species of the Pacific coast of North America will be considered later. The investigation falls into two parts. Beaches around the south and south-western coasts of England and Wales have been examined and the ecological conditions prevailing on each, more particularly the nature of the substratum and the salinity of the water, have been compared and related to the presence or absence of *N. cirrosa* and *N. hombergi*. Following this, we have considered in rather more detail, the ecology of a number of beaches of various types, which contain one or other or both species of *Nephtys*.

METHODS

(*a*) *General procedure*

The survey of beaches was made in the autumn, winter and spring of 1958-59. Most of the beaches were visited only once. Each has been examined during the period around low water and, while no special attempt has been made to collect

* Permanent address: Department of Zoology, Peninsular College, Monterey, California.

in the lowest intertidal zone, no collections have been made during the week of neap tides, so that most tidal levels have been investigated. It has been found that *Nephtys* may occur at almost any tidal level and that even on an apparently uniform and homogeneous beach its distribution is patchy. Consequently diggings have been made at as many sites on a beach as time permitted. It was originally intended to collect about fifty specimens from every beach on which the worms occurred so that if there was a mixture of species, a reasonable estimate could be made of the proportions of each. This proved totally impracticable at most beaches, in some of which only a single specimen was found after 2 or 3 h digging and sieving. In practice, every beach has been dug over for at least an hour and generally for two or three, and all the *Nephtys* seen have been collected. The intensity of search on a beach has been almost inversely proportional to the number of *Nephtys* found on it. A sample of the substratum has been taken for analysis at the place where the worms were most abundant, or, on beaches where the worms were rare, some sand was collected at each place where a worm was found. The sample of the substratum was collected between mean tide level and the low-water mark on the beaches where no *Nephtys* were found. No special attention has been directed towards other members of the fauna, though the most abundant and conspicuous animals have been recorded.

(*b*) *Soil analysis*

No standard method of the mechanical analysis of marine sediments has yet been evolved. Most previous investigators of the relationship between the composition of marine deposits and the animals that live in them have graded the soil by a combination of sieving, elutriation and sedimentation methods and have adopted the Wentworth (1922) scale of grade size. However, no two investigators have graded the soil in exactly the same way and it is impossible to make more than a rough comparison of their results. The problems of soil analysis have been discussed by Beanland (1940), Holme (1949, 1954) and Morgans (1956) among others. It seems bad practice to subject the soil to the pre-treatment usually employed by agriculturalists before grading, because this separates the smallest particles of soil that are aggregated into crumbs in the undisturbed marine soil (Morgans 1956) and, since the biological and physical importance of grades of a particular size is almost completely unknown, it appears that much of the labour of isolating the finest grades of soil is superfluous or at best of unproved value. Webb (1958) has recently shown that the permeability properties of marine soils change drastically when the size of grains falls below 0·2 mm, and that grains between 0·3 and 0·2 mm in diameter are important in the formation of quicksands. He has therefore proposed an entirely different series of sieves for sand analysis in ecological work from that used by previous investigators.

Unfortunately, we did not encounter Webb's suggestions until after the present survey had already started and a different series of sieves was already in use. We have adopted the following procedure. The sample of about 500 g of substratum was oven dried at 105° C overnight and then graded through the following series

of wire sieves: 2·000, 1·000, 0·500, 0·250, 0·125, 0·062 and 0·037 mm. The relative size of each fraction retained by the sieves is expressed as a percentage by weight of the total sample. The fractions retained by each sieve are described as granule, very coarse sand, coarse sand, medium sand, fine sand, very fine sand, and silt, respectively, in Wentworth's classification.

(*c*) *Salinity determinations*

A sample of 400 ml sea-water was taken, generally from the water's edge at low water. It was kept in a sealed bottle and analysed within 36 h. The simple procedure recommended by Harvey (1945) has been followed. Three 10 ml aliquots of sea-water were titrated against silver nitrate solution (27·25 g/l), using potassium dichromate as an indicator.

(*d*) *Transects*

On the beaches that were examined in greater detail, transects have been made with stations equally spaced from H W M O T to low water. At each station, two 0·5 m squares were marked out with a metal frame and the enclosed sand dug out to a depth of 15 cm, washed through a 2 mm wire sieve and the animals picked out and preserved. A sample of soil was collected either at each station or at selected stations and graded by the procedure outlined above. On the Gann Flats at Dale, additional transects were made across the beach at different tidal levels and here 1 m squares were dug out.

THE DISTRIBUTION OF *NEPHTYS* AROUND THE COAST

(*a*) *The faunistic survey*

The intertidal distribution of *Nephtys* around the south and south-western coast of England and the South Wales coast is shown in Fig. 1. Only the two species *N. cirrosa* and *N. hombergi* have been found to occur commonly. Except at a few localities, the two species do not occur together on the same beach and a clear pattern of the distribution of each of them emerges from the survey. Details of the beaches that have been visited and of the fauna associated with *Nephtys* are given in the Appendix.

N. hombergi has been found on the southern shore of the Bristol Channel between Stolford and Portishead, where conditions are estuarine. It does not occur on the Welsh side of the Channel. It occurs in semi-estuarine conditions at Dale, in Pembrokeshire, and also in the Tamar, Salcombe and Exe estuaries on the south coast of England. It has been found in the intertidal zone of shores on the open coast only at Swansea, Marazion, Seaton Beach, Torquay and Langstone Rock, and at each of these localities it is associated with *N. cirrosa*.

N. cirrosa is the characteristic species of marine sandy beaches. It occurs at the mouths of the Salcombe and Exe estuaries where it overlaps the range of *N. hombergi* and the two species occur together on the same beaches at Salcombe and Dawlish Warren. It penetrates into the Bristol Channel as far as Limpert

Bay and Blue Anchor on the north and south shores respectively. Here there is no overlap with the range of *N. hombergi* because the latter species does not occur on the Welsh side of the Channel, and there are no suitable beaches where *Nephtys*

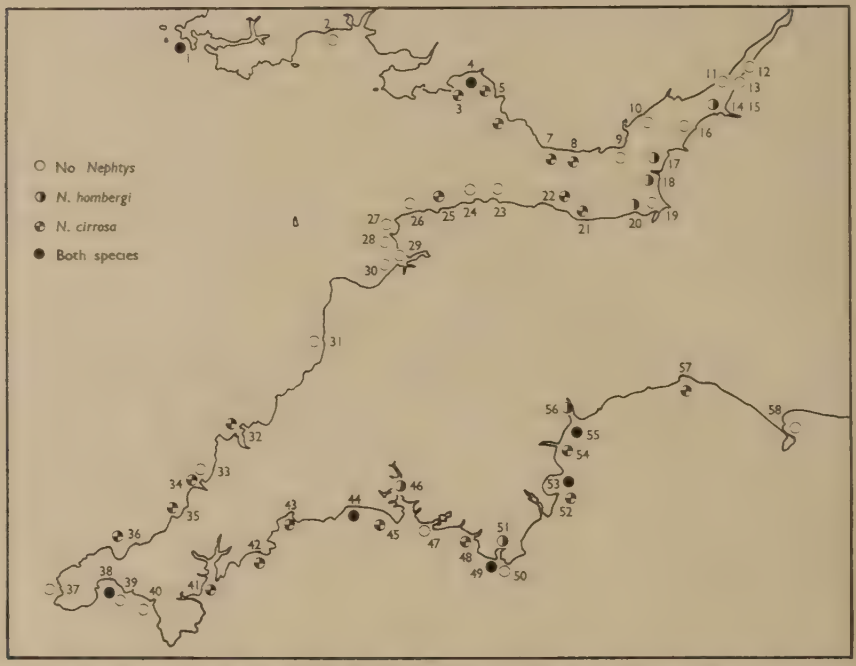


Fig. 1. Distribution of *Nephtys cirrosa* and *N. hombergi* on beaches around the south-west coast of Britain. Numbers refer to the collecting sites.

1. Dale
2. Pendine
3. The Mumbles
4. Swansea
5. Port Talbot
6. Porthcawl
7. Llantwit Major
8. Limpert Bay
9. Sully
10. Peterstone Wentlooge
11. Portskewett
12. Aust
13. Sugarhole Sands
14. Portishead (Royal Beach)
15. Portishead (Kilkenny Bay)
16. Clevedon
17. Weston-super-Mare
18. Brean
19. Steart
20. Stolford
21. Blue Anchor
22. Minehead
23. Sillery Sands
24. Lynmouth
25. Combe Martin
26. Ilfracombe
27. Woolacombe Sands
28. Croyde Bay
29. Instow
30. Westward Ho!
31. Bude
32. Pentireglaze
33. Newquay Bay
34. Fistral Bay
35. Perranporth
36. Carbis Bay
37. Sennen Cove
38. Marazion
39. Prah Sands
40. Porthleven
41. Maen Porth
42. Porthluney Cove
43. Par
44. Seaton Beach
45. Whitesand Bay
46. Tamar estuary
47. Wembury
48. Bigbury
49. Salcombe
50. E. Portlemouth
51. Upper Salcombe estuary
52. Paignton
53. Torquay
54. Teignmouth
55. Langstone Rock (Dawlish)
56. Exe estuary
57. Lyme Regis
58. Weymouth

might live between Blue Anchor and Stolford on the Somerset coast, where such an overlap might be expected. *N. cirrosa* is fairly common on sandy beaches on the north Somerset coast west of Blue Anchor and on all the beaches we have examined on the south coast of England between the Lizard and Dawlish, but

east of the Exe estuary the beaches are composed of pebble and gravel rather than sand, and provide few suitable intertidal habitats for *Nephtys*. The beaches of South Wales between the Mumbles and Limpert Bay also contain colonies of this species. The Lizard and the north coast of Devon and Cornwall are exposed, are generally rocky, and include relatively few sandy beaches. These contain at most only a few *N. cirrosa* and generally none at all. The beaches at Combe Martin, Pentireglaze and Marazion are protected, however, and all three have large colonies of *N. cirrosa*. The south coast of west Wales is also exposed and probably much the same conditions prevail as on beaches of the north coast of Devon and Cornwall. The only such exposed beach that we examined, at Pendine, contained no *Nephtys*.

N. caeca (O. F. Müller) has been reported from a few scattered localities on the south and south-western coasts of Britain. Single specimens have been recorded from Dale (Bassindale & Barrett 1957), Llantwit Major (Purchon 1947), in Plymouth Sound (Marine Biological Association 1957), and it was found in numbers at East Portlemouth by Allen & Todd (1900). We have not been able to confirm any of these records, although all the localities, except those in Plymouth Sound, have been reinvestigated. The colony at East Portlemouth seems to have disappeared during the changes in the substratum that followed the death of the *Zostera* in the Salcombe estuary (Wilson 1949) and no *Nephtys* of any species were found on that beach during the present survey. *N. caeca* is an arctic and circumpolar species and appears to have at most only a scattered, temporary and infrequent distribution on the western and southern coasts of Britain. It can be excluded from further discussion.

One specimen of *N. longosetosa* Oersted was collected at Port Talbot. Like *N. caeca*, this arctic species occurs infrequently and sporadically on the south and west coasts of Britain.

From this survey, it appears that *N. hombergi* is a species of the lower reaches of estuaries and that *N. cirrosa* replaces it on marine sandy beaches. Neither species lives on beaches where the wave action is severe. Two features of the mouths of estuaries are a reduced and widely fluctuating salinity and the deposition of silt, while the beaches exposed to severe wave action contain no silt and relatively few fine particles in the substratum. The salinity and the substratum are therefore the two factors most likely to be responsible for the different distribution of the two species.

(*b*) *The influence of salinity on the distribution of* Nephtys

The measurement of salinity conditions on a beach is beset with difficulties. Isolated measurements of salinity in estuaries have little value because of seasonal and tidal fluctuations and the possible stratification of salt- and fresh-water. Since it has been impracticable to make a detailed study of the salinity variations at each beach where collections of worms were made, we have taken a single sample at each beach at low tide from the water's edge. In estuaries, this probably represents the lowest salinity prevailing at that time of year. Fortunately,

salinity fluctuations in the Bristol Channel and the Tamar and Exe estuaries have been studied in various degrees of detail by Bassindale (1943a), Milne (1938) and Holme (1949), respectively, so that by combining our observations with theirs, it is possible to arrive at a conclusion about the salinity conditions at the estuarine stations.

Another problem which is less easily solved has been to decide what salinity measurements would be the most relevant to our study. Measurements of the salinity of the sea-water do not necessarily reflect the salinity of the water to which the animals living in the substratum are exposed. Some animals, such as *Nereis diversicolor*, are under the influence of the interstitial water which may have a

Table 1. *Salinity tolerance of* Nephtys hombergi *and* N. cirrosa

Salinity apparently within tolerance range						Salinity below tolerance range	
Worms present				Worms absent			
	S‰		S‰		S‰		S‰
Nephtys hombergi							
Portishead	15·9			Clevedon	21·5	Severn Beach	5·3
Weston-s-Mare	23·7			Combe Martin	21·9	Aust	13·2
Brean	28·8			Par	21·9		
Stolford	25·1			Steart	25·1		
N. cirrosa							
Maen Porth	4·5	Porthcawl	29·5	Pendine	28·0	Severn Beach	5·3
Combe Martin	21·9	Llantwit Major	30·0	Lynmouth	30·6	Aust	13·2
Par	21·9	Port Talbot	30·8	Porthleven	32·5	Portishead	15·9
The Mumbles	26·3	Perranporth	31·3	Prah Sands	32·7	Clevedon	21·5
Limpert Bay	27·2	Weymouth	33·3	Woolacombe	33·2	Weston-s-Mare	23·7
Porthluney	27·6	Pentireglaze	34·4	Bude	33·5	Instow	23·7
Lyme Regis	28·2	Fistral Bay	35·0	Croyde Bay	33·5	Brean	23·8
Minehead	28·4	Paignton	35·0	Weymouth	33·5	Steart	25·1
Blue Anchor	29·4	Teignmouth	35·0	Sillery Sands	33·6	Stolford	25·1
Carbis Bay	29·4			Westward Ho!	34·5		
				Ilfracombe	35·0		
Beaches containing both species				Newquay Bay	35·0		
				Sennen	35·0		
Swansea	24·6	Marazion	32·6				
Lower Exe estuary		Langstone Rock	35·0				
Dawlish Warren	30·0	Torquay	35·0				
Seaton Beach	31·5						

considerably lower salinity than that of the sea when a freshwater stream drains into the beach (Smith 1955) but others are primarily influenced by the supernatant water. *Nephtys* does not consolidate the walls of its burrow with mucus and on this account is likely to be influenced principally by the salinity of the interstitial water, but since it lives very close to the surface of the substratum, the interstitial and supernatant water probably do not differ appreciably except on very poorly drained beaches.

The salinity of the water at low tide, measured at stations in the Bristol Channel where *N. hombergi* occurs, varied between 15·9‰ and 25·1‰ (Table 1). How close an approximation these values are to the salinities prevailing at each station during the year can be gauged from Bassindale's (1943a) data on seasonal and tidal

fluctuations in the Severn estuary. At Weston-super-Mare, which represents the middle of the local geographical as well as of the salinity range of this species, fluctuations in salinity are slight. The tidal fluctuation in summer is 0·1‰ and in winter 1·0‰. The seasonal fluctuation in salinity is from about 28‰ in late summer to 22‰ in early spring. Upstream, at Aust, the pattern of salinity fluctuation is quite different. During the summer the mean salinity is about 25‰, with a tidal fluctuation of 1-2‰; in winter the general salinity is reduced to about 12-14‰ and the tidal fluctuation is appreciable on neap tides, when the salinity may fall to 0‰, but on spring tides the fluctuation is only 1-2‰. The change in the pattern of salinity fluctuation is probably fairly abrupt and is likely to occur at Avonmouth, where the river bed narrows suddenly. The region between Clevedon and Portishead is a critical one beyond which marine animals do not penetrate, and at Portishead the occurrence of some marine species is variable and unpredictable. *Balanus improvisus* and *Sabellaria alveolata* are present in some years, but absent in others, for example (Bassindale 1943b); *Nephtys hombergi* is included among the marine animals that penetrate as far as the critical zone at Portishead, but no further upstream.

In the Tamar estuary, *N. hombergi* is common as far as Saltash, but its numbers decrease above this point (Spooner & Moore 1940) and it finally disappears at Pentillie Quay (Percival 1929). The salinity fluctuations at Weirmouth, just below Pentillie Quay, resemble those at Aust, and in winter the surface salinity may fall to 1‰ on a low tide and rise to 23‰ at high water. In summer the salinity at high water reaches 26‰ (Milne 1938). *N. hombergi* is common in the Salcombe estuary from Millbay and Sandhill Point, near the mouth of the harbour, to Gerston Point (Allen & Todd 1900). No detailed information about the salinity variations in this estuary is available, but the rivers flowing into it are small and conditions in it appear to be essentially marine. Measurements of salinity in mid-stream at high and low water in August and October suggest that there is no substantial seasonal fluctuation (Allen & Todd 1900). In the Exe estuary, *N. hombergi* penetrates as far as Powderham (Allen & Todd 1902). Surface salinities measured by Holme (1949) indicate that the salinity at Powderham reaches 30-32‰ on high tides in summer and autumn, but on low tides falls to 21-25‰. Upstream from Powderham, the salinity fluctuations are much greater, and at Turf the surface water is almost fresh at neap tides in March. The region immediately above Powderham therefore represents a critical zone comparable to the region above Portishead in the Bristol Channel and between Saltash and Wiermouth in the Tamar estuary.

This species therefore penetrates into estuaries as far as the region where tidal fluctuations in salinity in winter are considerable, but the limit of its range in the lower part of the estuary is clearly not related to salinity. It is not exclusively an estuarine species, but occurs on marine beaches at Swansea, Marazion, Seaton Beach, Torquay and Langstone Rock (Table 1) and is also common in sublittoral deposits in the Irish Sea and the Firth of Clyde (Clark & Milne 1955, Clark 1960).

N. cirrosa does not occur in any of the estuaries around the coast, except that of the Exe in which it has been found at a number of sites near the mouth of the

estuary (Allen & Todd 1902, Holme 1949), where the salinity does not fall below about 30‰ (Holme 1949). It occurs also at Salcombe, but conditions there are essentially marine. In the Bristol Channel it penetrates as far as Sully on the Welsh coast to Blue Anchor on the English side. Because the river channel is closer to the Somerset coast and the Welsh coastline is exposed to the south-westerly storms estuarine conditions persist as far as Stolford, and to a diminishing extent to Minehead on the south shore of the Channel, but only to Sully on the north (Haderlie & Clark 1959). We have not generally found *N. cirrosa* where the measured salinity was below 26·3‰ (Table 1). At Maen Porth, where the very low salinity of 4·5‰ was recorded, a considerable volume of fresh-water ran across the beach and because of the sheltered conditions and the very still weather on the day that the beach was visited, it apparently did not mix appreciably with the sea-water. As Reid (1930) demonstrated, fresh-water running over sand may have remarkably little effect on the salinity of the interstitial water to which the animals are exposed. A considerable amount of fresh-water runs across a number of other beaches that were examined (*e.g.* Ilfracombe, Bude, Prah Sands), but there appears to have been sufficient mixing with sea-water in the surf for it not to influence the salinity measurements appreciably. The reduced salinity at Seaton Beach is attributable partly to the fresh-water running across the beach and partly to the local influence of a small stream. The low salinity measured at Par appears to be a true representation of the conditions prevailing there, and the beach is evidently not very suitable for *N. cirrosa* because only two specimens were found there after prolonged digging.

(*c*) *The influence of the substratum on the distribution of* Nephtys

In grading the soil it has been found that the greatest fraction is composed of particles between 0·25 and 0·125 mm diameter and the chief differences between the substrata lie in the proportion of particles coarser and finer than this fraction. The following discussion can be simplified by paying greatest attention to the coarse (>0·25 mm) and fine (<0·125 mm) grades.

N. hombergi has been found on beaches composed of muddy sand in which there is between 2·24 and 15·89% fine material and between 0.12 and 3·82% coarse particles (Table 2). The greatest numbers were found at Brean, where the substratum contains 5·84% fine and 0·29% coarse material. *N. cirrosa* occurs in clean sand in which there is between 1·56 and 88·58% coarse material, and not more than 6·6% fine particles (Table 2). Most of the beaches inhabited by this species contain less than 1·8% fine material and more than 4·5% coarse material in the substratum, but the analyses of the four relatively fine substrata inhabited by *N. cirrosa* are instructive. The substrata at Lyme Regis, Combe Martin and the Mumbles all have the same proportion of fine particles (3·42%). That at Lyme Regis has only 1·56% coarse particles and appears to be more suitable for *N. hombergi* than *N. cirrosa* and in fact only one specimen of the latter species was found there. It is not clear why *N. hombergi* should not have colonized the beach.

But at Combe Martin and the Mumbles the sand contains 40 and 80% of coarse material, and both beaches have numerous populations of *N. cirrosa*. Evidently the presence of coarse material in the substratum mitigates the discouraging effect of a high silt content on this species. This is apparently the explanation of the large colony of *N. cirrosa* at Minehead I, where the substratum contains 6·6% fine material and 3·23% coarse particles. This is one of the finest substrata inhabited by *N. cirrosa* and the beach has been investigated in some detail (see p. 129). Beaches with more than 50% coarse particles generally contain few *Nephtys*, though there are large colonies of *N. cirrosa* at Teignmouth and Whitesand Bay, where the substratum contains 69 and 76% coarse particles respectively, and the species is fairly common at Swansea, Port Talbot and Llantwit Major, which also have relatively coarse substrata.

The most usual substratum in which *N. cirrosa* occurs therefore contains less than 1·8% fine particles and between 4 and 50% coarse material, but this species is tolerant of substrata containing a greater proportion of fine particles, providing there is an admixture of coarse particles with the fine. The densest colony of *N. cirrosa* is at Blue Anchor, where the substratum contains 1·71% fine material and 6·66% coarse material.

The beaches where both *N. cirrosa* and *N. hombergi* live in the same substratum are of particular interest. These are at Swansea, Marazion, Seaton Beach, Salcombe, Torquay and Langstone Rock (Table 2). Seaton Beach is composed of very silty sand in which there is 12·40% fine material. It therefore contains a greater percentage of fine particles than is usual in beaches inhabited even by *N. hombergi*, but it also contains a large quantity of coarse material and in this respect is more characteristic of beaches populated by *N. cirrosa*. As we have seen at the Mumbles and Combe Martin, the admixture of a large proportion of coarse material in a generally silty beach renders the substratum tolerable for *N. cirrosa* and, in fact, at Seaton Beach there is a large population of this species and only a few, large *N. hombergi* near low-water mark. The other beaches are clearly more suitable for *N. cirrosa* than *N. hombergi* and at Salcombe and Langstone Rock the former species greatly outnumbers the latter. At Marazion, Torquay and Swansea, the two species are more nearly balanced in numbers, but there is still a preponderance of *N. cirrosa*. Holme (1949) found both species to occur in the lower part of the Exe estuary, on the inner side of Dawlish Warren. Because of the different mesh sizes employed in the mechanical analysis of the substratum it is impossible to make a close comparison of his results with our own analyses, but it is clear that the substratum on the inner side of the Warren is also relatively poorly sorted, as at Seaton Beach, but that it contains a far higher proportion of silt than the substratum at Seaton. Although both species are present on the inner side of Dawlish Warren, *N. hombergi* occurs in greater numbers than *N. cirrosa*, and this appears to be a result of the high proportion of silt in the substratum.

The remaining beaches in which no *Nephtys* have been found can be divided into three groups (Table 2): those too silty even for *N. hombergi* (Peterstone Wentlooge, Portskewett, Aust, Sugarhole Sands and the mud at Clevedon);

Table 2. *Mechanical analysis of beach substrata*

Figures show the percentage of material in each fraction.

	Particle size (mm)									
	Coarse >0·25	Fine <0·125	>2·0	2·0-1·0	1·0-0·5	0·5-0·25	0·25-0·125	0·125-0·062	0·062-0·037	<0·037
Beaches containing *Nephtys hombergi*:										
Portishead, Kilkenny Bay	0·12	15·89	–	–	–	0·12	84·43	7·61	5·32	2·94
Brean	0·29	5·84		0·03	0·08	0·18	93·87	4·41	0·98	0·45
Weston-super-Mare	3·82	4·73	0·35	0·39	0·22	2·86	91·45	2·65	1·69	0·39
Stolford	2·65	3·07	0·04	0·13	0·24	2·24	94·28	2·48	0·29	0·30
Portishead, Royal Beach	0·28	2·24	–	–	0·02	0·26	97·51	1·72	0·35	0·17
Beaches containing *N. cirrosa*:										
Minehead I	3·23	6·60				(*See* Table 3)				
Lyme Regis	1·56	3·42	–	0·02	0·12	1·32	95·12	2·83	0·49	0·10
Combe Martin	40·42	3·42	3·92	2·57	4·25	29·68	56·17	2·91	0·44	0·07
The Mumbles	80·05	3·42	0·98	2·38	5·95	70·74	16·53	1·84	1·00	0·58
Limpert Bay	66·93	1·78	0·28	0·34	1·21	65·10	31·30	1·33	0·35	0·10
Minehead II	6·06	1·71	–	0·07	0·25	5·74	92·24	1·21	0·39	0·11
Port Talbot	72·72	1·65	1·40	1·05	3·04	67·23	25·62	1·59	0·06	–
Blue Anchor	4·08	1·44	0·34	0·18	0·20	3·36	94·49	1·10	0·18	0·16
Llantwit Major	87·57	1·34	0·05	0·55	3·75	83·22	11·09	1·32	–	0·02
Porthcawl	73·02	1·21	3·21	1·43	3·05	65·33	25·77	1·16	0·05	–
Par	69·85	1·15	1·48	3·66	12·47	52·24	28·98	1·03	0·12	–
Paignton	24·01	1·02	3·03	2·78	2·27	15·91	74·99	0·97	0·05	–
Fistral Bay, Newquay	59·46	0·81	0·10	1·35	6·31	51·70	39·72	0·79	0·02	–
Bigbury	44·47	0·77	0·70	0·74	3·88	39·15	54·78	0·69	0·08	–
Maen Porth	48·19	0·56	0·91	1·33	2·83	43·12	51·26	0·56	–	–
Teignmouth	68·87	0·54	14·18	13·16	15·75	24·78	31·60	0·52	0·02	–
Pentireglaze	11·98	0·43	–	0·02	0·62	11·43	87·58	0·41	0·02	–
Whitesand Bay	75·94	0·18	0·21	0·53	4·17	71·03	23·88	0·16	0·02	–
Porthluney Cove	63·76	0·14	2·33	2·71	7·59	51·13	36·10	0·14	–	–
Carbis Bay	80·84	0·14	0·22	0·69	7·05	72·88	19·00	0·12	0·02	–
Perranporth	85·58	0·05	0·02	0·21	3·77	84·58	11·37	0·05	–	–

Beaches containing both species:										
Seaton Beach	5·57	12·40	0·12	0·05	0·07	5·53	81·82	11·11	1·12	1·17
Swansea	77·03	1·75	0·44	0·33	0·71	75·55	21·23	1·33	0·23	0·19
Marazion	5·30	1·57	0·11	0·17	0·51	4·51	93·13	1·55	0·02	–
Salcombe	56·33	1·55	2·28	4·45	6·69	42·91	42·13	1·29	0·22	0·04
Langstone Rock	71·17	0·35	6·28	4·90	4·85	55·14	28·49	0·33	0·02	–
Torquay					(*See* Table 4)					
Beaches containing neither species:										
Peterstone Wentlooge	–	100·00								
Portskewett	–	100·00								
Aust	–	100·00								
Sugarhole Sands	–	100·00								
Clevedon (mud)	–	100·00								
Sully	15·26	6·84	2·98	0·69	1·15	10·44	77·90	6·00	0·61	0·23
Steart	4·71	2·81	–	0·02	0·12	4·47	93·59	0·94	0·61	0·26
East Portlemouth	48·32	2·62	0·25	0·36	3·01	44·70	48·98	2·22	0·30	0·10
Instow	9·69	2·15	–	0·04	0·43	9·22	88·15	1·80	0·31	0·04
Pendine	18·84	1·91	1·24	1·18	2·05	14·37	79·25	1·65	0·26	–
Sillery Sands	55·13	1·65	0·44	1·52	8·68	44·49	43·22	1·46	0·13	0·06
Westward Ho!	19·04	0·85	–	–	0·38	18·66	80·10	0·76	0·09	–
Weymouth	1·33	0·83	–	0·03	0·50	0·80	98·29	0·80	0·03	–
Wembury	79·19	0·46	0·49	0·97	7·33	70·70	20·04	0·38	0·06	0·02
Newquay Bay	60·05	0·21	2·10	2·68	5·84	49·43	39·75	0·21	–	
Woolacombe	84·32	0·93	0·57	1·74	4·46	77·55	15·47	0·91	0·02	–
Croyde	93·50	0·06	0·10	0·51	4·84	88·05	6·44	0·06	–	–
Prah Sands	95·98	0·04	0·42	2·04	23·58	69·94	3·98	0·04	–	–
Bude	95·98	0·03	0·46	0·77	18·97	74·77	3·99	0·03		
Sennen	99·36	0·02	0·02	0·68	51·53	47·12	0·62	0·02	–	–
Ilfracombe	99·37	0·03	10·59	45·86	32·78	10·15	0·60	0·03	–	
Lynmouth	99·65	0·06	14·51	32·67	45·53	6·93	0·29	0·06	–	–
Clevedon (gravel)	100·00	–								
Porthleven	100·00	–								

those too coarse for *N. cirrosa* (Croyde Bay, Bude, Prah Sands, Sennen, Ilfracombe, Lynmouth, the gravel at Clevedon, Porthleven, and possibly Woolacombe); and those beaches whose substrata appear to be suitable for one or other species of *Nephtys*. The conditions on each of these must be considered separately.

Although at Pendine, Sillery Sands, Westward Ho! and Newquay Bay the substratum has a suitable grade composition for *N. cirrosa*, the coarser fractions are composed of sharp shell fragments. These beaches are exposed to severe wave action and we have never found any species of *Nephtys* living under these conditions. Some other beaches in north Cornwall (Perranporth, Carbis Bay, Fistral Bay) have a comparable substratum and although *N. cirrosa* does occur in the sand, it is extremely rare.

At Wembury, although the coarser fractions of the substratum do not contain a very large quantity of shell fragments, the sand is coarse and the beach is exposed to severe wave action. While *N. cirrosa* has been found in as coarse, or coarser substrata at Llantwit Major, Perranporth and Carbis Bay, it is not common in them and they clearly represent an unsuitable environment for the worm.

At East Portlemouth the beach once contained a large population of *N. caeca* (Allen & Todd 1900), but conditions there have changed since the death of the *Zostera* (Wilson 1949) and the sand is practically devoid of animals. The substratum has an unusual spongy texture, and according to Wilson a considerable amount of erosion is taking place in the harbour, and sand is being deposited on other parts of the beach, particularly at Ditch End corner.

At Weymouth the substratum is well sorted and the particles comprising it are remarkably uniform in size. The substratum does not fall readily into either of the types by *Nephtys cirrosa* or *N. hombergi*. It is probably too fine for *N. cirrosa* since it contains even fewer coarse particles than the substratum at Lyme Regis where this species is rare, and contains too few fine particles to be suitable for *N. hombergi*. The possibility that one or other species occurs at Weymouth remains, however, since only the upper half of the beach was examined.

The substratum at both Instow and Steart is rather silty for *N. cirrosa*, but falls within the extreme range for the species. It is coarser than that usually inhabited by *N. hombergi*. At both places the salinity is below the normal range for *N. cirrosa* (Table 1), and *Nereis diversicolor* is present in large numbers. The combination of low salinity and silty substratum probably excludes *Nephtys cirrosa* from what would in any case be a suboptimal environment.

Although the composition of the sand at Sully appears to be suitable for its colonization by *N. hombergi*, it occurs only in small pockets in a generally gravelly beach. There is a deposition of fine silt over the whole beach, particularly towards L W M.

THE INTERTIDAL DISTRIBUTION OF *NEPHTYS*

A more detailed examination of the occurrence of *Nephtys* in relation to tidal level, the composition of the substratum and the accompanying fauna has been made at Brean, where only *N. hombergi* occurs, at Minehead, where *N. cirrosa* is abundant, at Torquay, where both species occur on a beach with a uniform substratum,

and at Dale, where both species occur on a beach with a very varied and patchy substratum. These results are compared with the distribution of *N. hombergi* and *N. cirrosa* at Millport, where both the intertidal and the sublittoral distribution of the worms has previously been investigated.

(*a*) *Brean, Somerset*

The beach is flat below H W N; above this there is a pebble and shingle bank some 2 m high. On spring tides the water recedes nearly 1500 m, exposing sand in the upper 200 m grading into fine mud which comprises the lower three-quarters of the beach. This mud is very soft and has proved inaccessible. Stations were marked at 50 m intervals on a transect from H W N to the edge of the mud-flats (Fig. 2). The fauna is a very limited one, but there is a clear intertidal zonation of the commoner species. *N. hombergi* occurs over a broad region in the middle part of the beach and attains its greatest numbers immediately below the densest part of the bed of *Arenicola marina*. The substratum at Brean is coarsest at H W N and

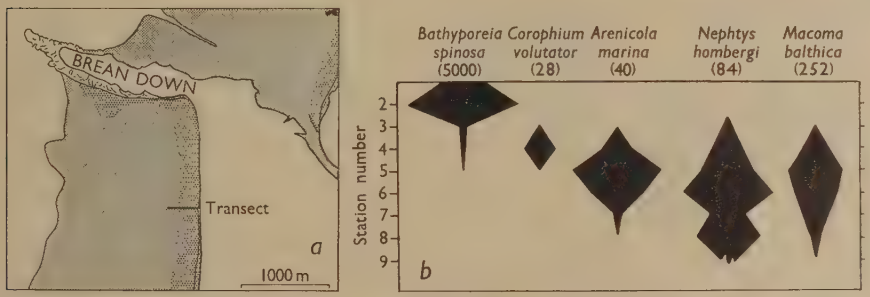


Fig. 2. *a*, Brean, Somerset, showing the position of the transect. Fine stipple, mud; coarse stipple, sand. High-water and low-water marks of ordinary tides are indicated.

b, Distribution of the commonest animals in the beach at Brean. Scales various. The number at the head of each polygon represents the maximum density (animals per m²) of that species in the transect.

becomes steadily finer towards M T L (Table 3). The substratum at the two highest stations appears to be too coarse for this species and the substratum at Station 6, where the greatest density of worms is attained, falls well within the normal range for this species in its composition (Table 2).

(*b*) *Minehead, Somerset*

The beach at Minehead was selected for detailed study because it contains one of the densest populations of *Nephtys cirrosa* that we have encountered. It is also interesting because the substratum is finer than that usually inhabited by *N. cirrosa*.

The beach is composed of a narrow shingle bank 2 m high, at H W N, with tongues of gravel and small rocks running across the beach to L W S. There are two extensive areas of sand between the gravel banks, one, known as The Strand, where the transect was made (Fig. 3) and included in Table 2 as 'Minehead I', and another further to the east known as Madbrain Sands, designated 'Minehead II'. The latter

is a little more exposed and the substratum is coarser than on The Strand (Table 2). There are large populations of *N. cirrosa* in both sandy areas. On spring tides the water recedes about 800 m from the shingle bank, exposing, at least on The Strand, an area of heavy blue clay between L W N and L W S. A very thin layer of silt is deposited on the clay in places, but much of it is scoured clear of any deposit. For 100-150 m above L W N the clay is covered by a layer of sand varying between 5 and 30 cm in depth. Collections were made over a wide area of Madbrain Sands, and a transect with stations at 50 m intervals, starting 25 m from the foot of the shingle bank and ending in the middle of the blue clay, was made on The Strand. The chief members of the fauna and their intertidal distribution are shown in

Table 3. *Analysis of substrata and the intertidal distribution of* Nephtys

Stn	Distance from HWN (m)	Number of *Nephtys* per m²	Analysis of substratum: % in each size (mm) fraction									
			Coarse >0·25	Fine <0·125	>2·0	2·0-1·0	1·0-0·5	0·5-0·25	0·25-0·125	0·125-0·062	0·062-0·037	<0·037
N. hombergi at Brean:												
1	0	0	3·18	0·59	0·02	0·02	0·04	3·10	96·22	0·57	0·02	–
2	50	0	3·18	0·59	0·02	0·02	0·04	3·10	96·22	0·57	0·02	–
3	100	8	0·85	4·89	0·02	0·04	0·06	0·73	94·27	4·81	0·06	0·02
4	150	28	0·73	1·82	0·02	0·04	0·06	0·61	97·45	1·53	0·19	0·10
5	200	48	0·62	7·24	0·04	0·02	0·04	0·52	92·15	5·38	1·67	0·19
6	250	84	0·29	5·84	–	0·03	0·08	0·18	93·87	4·41	0·98	0·45
7	300	32	0·60	9·40	–	0·07	0·07	0·46	90·00	8·44	0·60	0·36
8	350	56	0·25	19·82	–	–	0·04	0·21	79·93	16·88	1·89	1·05
9	400	16	1·48	33·89	–	–	0·13	1·35	64·63	26·69	5·85	1·35
N. cirrosa at Minehead:												
1	25	0	11·48	1·04	–	0·15	0·18	11·15	87·47	0·89	0·09	0·06
2	75	0	15·22	1·14	0·49	0·24	1·31	13·18	83·65	0·92	0·11	0·11
3	125	8	34·90	1·69	11·40	0·75	2·07	20·68	63·41	1·72	0·22	0·20
4	175	10	13·74	3·33	3·06	0·99	1·43	8·26	82·93	2·96	0·26	0·11
5	225	18	7·33	3·72	2·94	0·47	0·78	4·70	87·39	3·09	0·39	0·24
6	275	28	5·34	7·24	0·62	0·22	0·44	4·06	87·24	6·67	0·44	0·31
7	325	42	4·87	7·01	0·04	0·18	0·22	4·43	88·13	6·27	0·48	0·26
8	375	56	3·23	6·60	0·04	0·04	0·25	2·90	90·17	6·02	0·33	0·25
9	425	12	1·32	2·87	0·11	0·11	0·15	0·95	95·81	2·61	0·15	0·11
10	475	54	0·97	2·48	0·30	0·16	0·23	0·28	96·54	2·32	0·09	0·07
11	525	0	–	100								
12	575	0	–	100								
13	625	0	–	100								
14	675	0	–	100								

Fig. 3*b*. *N. cirrosa* is present from Station 4 to the edge of the blue clay belt. Its numbers increase steadily and reach a maximum at Stations 9 and 11, just above L W N. Its relatively low density at Station 10 can be attributed to the fact that at this point there was less than 5 cm sand overlying the clay, whereas at the two neighbouring stations the sand was 15 cm deep. The distribution of this species is very similar to that at Torquay (Fig. 4) and Kames Bay (Fig. 6), save that the seaward extension of its range is prevented at Minehead by the lack of a suitable substratum below L W N. Unlike *N. hombergi*, it reaches its maximum numbers well below the densest part of the *Arenicola* zone.

From the analyses of the substratum at each station (Table 3), it appears that

the proportion of coarse material increases to a maximum at Station 3 and then decreases steadily towards L W M. The finer particles on the other hand form an increasing proportion of the substratum between Stations 1 and 6 and then decrease in importance towards L W M. The substratum as a whole is coarser than that at Brean (Table 3), where *Nephtys hombergi* is more abundant, and very little fine silt (<0·037 mm) is deposited at any station on the beach at Minehead. Station 10 (Table 3) and the area near L W M on Madbrain Sands (Table 2), where *N. cirrosa* achieves its greatest densities, both have substrata which fall within the normal range of the species, but Stations 7 and 8, where it is also abundant, present some difficulty because the substratum there contains 6-7% fine particles, which is outside the normal range of substrata containing *N. cirrosa* found in the faunistic survey (Table 2). The substratum at Station 8 contains 3·32% coarse particles and that at Station 7 4·87%, and, as we have already observed, the presence of

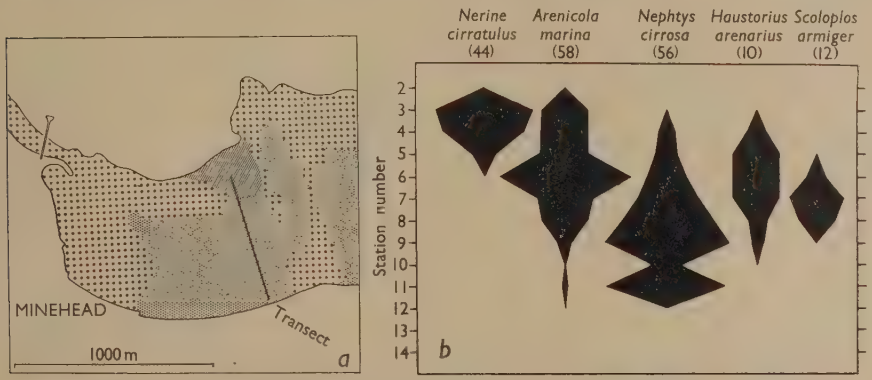


Fig. 3. *a*, Minehead, Somerset, showing the position of the transect. Fine stipple, sand; coarse stipple, gravel and rocks; cross-hatched, exposed blue clay. Low-water mark of ordinary tides is indicated. *b*, Distribution of the commonest animals on the beach at Minehead. Scales various. The number at the head of each polygon represents the maximum density (animals per m²) of that species in the transect.

coarse particles mixed with the fine material renders a silty substratum suitable for *N. cirrosa*. If the mechanical analysis of the substratum at Lyme Regis, where this species is rare, is compared with that at Station 8, it will be seen what a slight shift in the composition in the substratum permits its colonization by *N. cirrosa*.

(*c*) *Tor Abbey Sands, Torquay, Devon*

The entire beach at Tor Abbey Sands is entirely covered on all high tides when the water rises about 1·2 m up the sea wall. The beach is flat and the water recedes about 60 m on a normal spring tide. The whole beach lies beneath M T L. The harbour breakwater and the headland running out to Hope's Nose provide some protection to the east, and to the west of the collecting area there is a reef of rock covered with algae running to L W S, at Corbyn Head. Despite this degree of protection, the beach is exposed to considerable surf action. In the present survey,

twelve stations at 5 m intervals from the sea wall to low water were dug (Fig. 4). The fauna of the sand was described by Elwes (1909), who found that both *N. hombergi* and *N. cirrosa* occurred, the former lower down the beach than the latter, but in our examination of the beach we found both species to have approximately the same intertidal distribution (Fig. 4). The upper part of the beach contains *Arenicola marina* and *Nerine cirratulus* in a well-marked zone. As at Brean (Fig. 2), *Nephtys* first appears in the lower part of the *Arenicola* bed, but at Torquay the numbers of both species vary in a random way from station to station instead of showing a clear intertidal zonation. Analysis of the substratum at a number of stations (Table 4) shows that the sand over the whole beach is poorly sorted and contains large fractions of both coarse and fine material, as on the other beaches where both species occur together. There is no obvious relation between the composition of the substratum at each station and the relative numbers of each species.

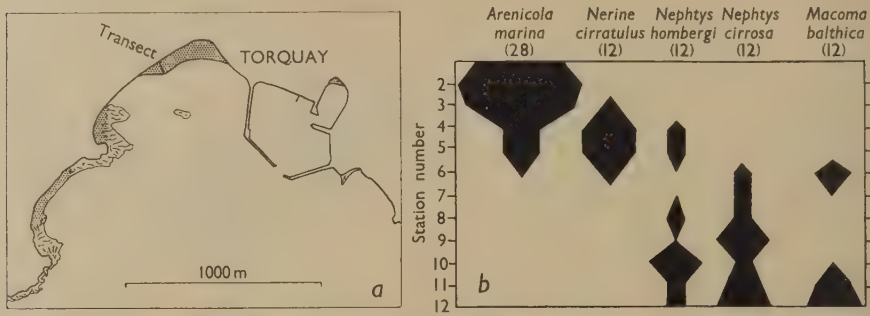


Fig. 4. *a*, Tor Abbey Sands, Torquay, Devon, showing the position of the transect. Fine stipple, sand. Low-water mark of ordinary tides is indicated.

b, Distribution of the commonest animals on the beach at Torquay. Scales various. The number at the head of each polygon represents the maximum density (animals per m^2) of that species in the transect.

The situation at Torquay recalls that in the lower Exe estuary, at Dawlish Warren, described by Holme (1949); both species occur on both beaches, though at Torquay, with its coarser substratum, *Nephtys cirrosa* predominates, while at Dawlish Warren *N. hombergi* is the more numerous. At Dawlish, Holme found both species occurred over a considerable part of the beach and that numbers varied widely and randomly from station to station. The substratum at Dawlish Warren, like that at Torquay, is poorly sorted, and Holme could find no relation between the composition of the substratum and the distribution of the two species.

(*d*) *Gann Flats, Dale, Pembrokeshire*

A more ambitious survey of the distribution of *Nephtys* was attempted on the Gann Flats, where both *N. cirrosa* and *N. hombergi* have been reported to occur (Bassindale & Barrett 1957). The flats occupy an almost rectangular bay over $\frac{1}{2}$ mile wide and $\frac{3}{4}$ mile long. It is sheltered, faces south-east and opens into Dale

Table 4. *Analysis of the substratum and the intertidal distribution of* Nephtys cirrosa *and* N. hombergi *at Torquay*

Stn.	Distance from sea-wall (m)	No. *N. cirrosa* per m²	No. *N. hombergi* per m²	Analysis of substratum: % in each size (mm) fraction								
				Coarse >0·25	Fine <0·125	>2·0	2·0-1·0	1·0-0·5	0·5-0·25	0·25-0·125	0·125-0·062	0·062-0·037	<0·037
1	0	0	0										
2	5	0	0	4·14	5·79	0·06	0·06	0·24	3·78	90·12	5·57	0·14	0·08
3	10	0	0	6·76	7·97	0·67	0·14	0·78	5·17	85·26	7·83	0·07	0·07
4	15	0	4										
5	20	0	4	4·98	2·86	0·05	0·05	0·44	4·44	92·15	2·82	0·02	0·02
6	25	4	0										
7	30	4	0	6·15	4·50	0·32	0·18	0·55	5·10	89·35	4·42	0·05	0·03
8	35	4	4										
9	40	12	0	10·13	3·87	1·16	0·55	1·45	5·97	87·00	3·71	0·11	0·05
10	45	4	12										
11	50	8	4	19·38	1·60	1·21	1·24	7·42	9·51	79·09	1·56	0·03	0·01
12	55	12	4										

Roads and thence into Milford Haven. The small River Gann flows on to the north corner of the beach and runs along the north-east side of a sand bank which runs down the centre of the beach. It does not drain into the sand until it reaches L W M O T and appears to have remarkably little effect on the fauna of the beach. The substratum is extremely varied and patchy so that a single transect drawn down the centre of the beach would provide almost no useful information about the distribution of the animals in it. Instead, several transects were made at

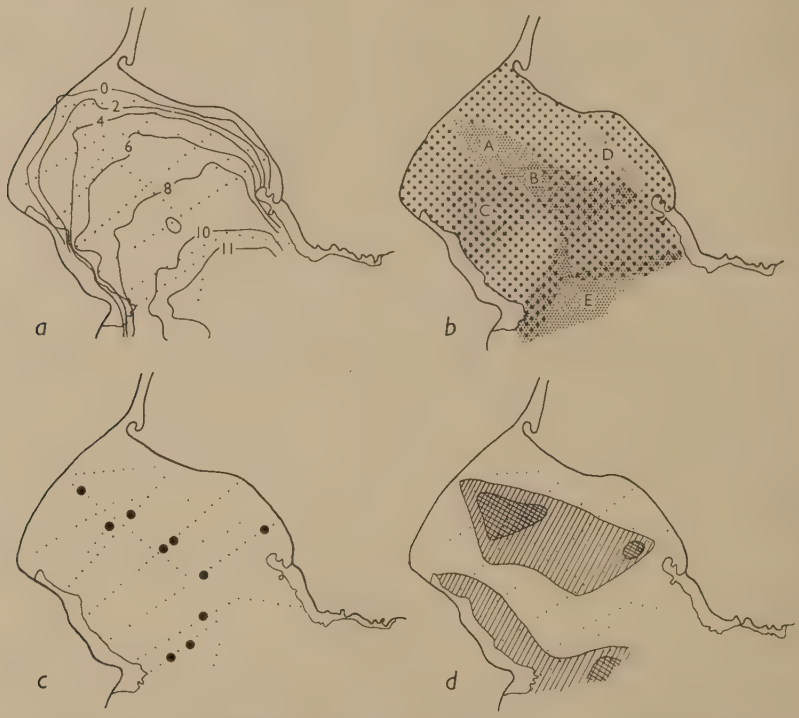


Fig. 5. The Gann Flats, Dale, Pembrokeshire. *a*, Levels, in feet, below ordnance datum. *b*, Nature of the substratum: fine stipple, mud; medium stipple, sand; coarse stipple gravel, pebble and stones. The letters indicate the positions at which soil samples were collected for analysis.
c, Distribution of *Nephtys cirrosa*. *d*, Distribution of *N. hombergi*. Small dots in *a*, *c* and *d* indicate positions of stations on the transects.

different tidal levels (Fig. 5). A subjective description of the substratum at and below the surface was made at each station and soil samples for analysis were collected at a number of strategic points (Fig. 5*b*). A detailed account of the ecology of the beach will be published elsewhere.

The beach shelves gradually (Fig. 5*a*) and on ordinary tides the water recedes to about 8 ft below datum; on exceptional spring tides it may fall more than 11 ft below the datum level at approximately H W N. The substratum (Fig. 5*b*) is composed chiefly of sandy or muddy gravel, though there is a gully filled with

fine mud on the north-east side of the beach (Station D) and a sand bank that runs down the centre of the beach (Station A). There are also small pockets of sand at the foot of the boulders lying along the south-west side of the beach. The substratum across the mouth of the bay is composed of sandy gravel on the south-west side, but becomes muddier towards the north-east side of the entrance; beyond this there is a sand bank which is exposed only on exceptional spring tides (Station E). Except in the upper part of the sand bank (Station A), the sandy gravel at the south entrance to the bay and the sublittoral sand bank (Station E), the substratum immediately beneath the surface is composed of black mud with a certain amount of gravel in it. This was found to be almost completely impermeable. An undisturbed core of substratum 1 cm in diameter and 4 cm long, consisting of 3 cm sand and 1 cm black mud, was set up under a 10 cm column of sea-water and no detectable quantity of water percolated through it in 12 h. Indeed, drainage over the whole beach is poor. Shallow pools of water lie on much of its surface throughout the low tide period and water from the upper part of the beach, the saltings that lie above H W S and from the River Gann drains across the beach rather than into it.

Both *N. cirrosa* (Fig. 5*c*) and *N. hombergi* (Fig. 5*d*) have been found in the present survey. The latter species predominates, but reaches a maximum density of only

Table 5. *Analysis of the substratum at selected points on the Gann Flats, Dale*

Stn.	Analysis of substratum: % in each size (mm) fraction									
	Coarse <0·25	Fine <0·125	>2·0	2·0-1·0	1·0-0·5	0·5-0·25	0·25-0·125	0·125-0·062	0·062-0·037	<0·037
A	25·11	8·43	0·98	4·69	5·75	13·68	66·46	6·63	1·6	0·64
B	2·82	14·52	0·63	0·42	0·60	1·20	82·63	12·38	1·51	0·63
C	85·04	3·65	63·43	7·87	4·71	9·03	11·31	1·91	1·51	0·59
C*	59·10	9·96	–	21·53	12·89	24·68	30·93	5·21	3·15	1·60
D	67·02	24·54	49·47	6·20	6·73	4·62	8·44	9·50	5·94	9·10
D*	34·73	48·57	–	12·27	13·32	9·14	16·71	18·80	11·75	18·02
E	0·37	13·00	–	–	0·22	0·15	86·62	12·77	0·23	–

* Percentages recalculated excluding the coarsest fraction (>2·0 mm).

11/m². No more than one or two specimens of *N. cirrosa* were found at any station. *N. hombergi* occurs in small numbers (<5/m²) on the sandbank that runs down the centre of the beach, in the pockets of sandy mud that lie along the south-west side of the beach and on the sublittoral sandbank. The greatest densities of this species are found in the upper part of the sandbank, where the substratum is of clean sand (Station A), but its numbers fall abruptly in the patch of muddy sand (Station B). The rest of the sandbank, which is generally gravelly, supports only small numbers of *N. hombergi* except in a small area of sandy gravel in the east corner of the beach, where the density is again relatively high. The worm does not occur in the muddy gravel at the eastern side of the entrance to the bay, but does in the sandy gravel on the south side of the entrance. *N. cirrosa* occurs only in the areas of clean sand or sandy gravel, but it is so scattered and in such small numbers that little can be concluded from its distribution on the beach.

The analyses of the substratum (Table 5) support what has previously been discovered about the preferences of the two species. The substratum at Stations A and E, where *N. hombergi* is most numerous, falls within the normal range for this species. Numbers are reduced at Station B, where the proportion of fine material in the substratum is increased. There are only small numbers of *N. hombergi* at Station C although there is only a moderate percentage of fine material in the substratum, but it should be noted that this fine fraction is composed of a greater proportion of fine silt (<0·037 mm) than at either Station A or Station E. Station D is clearly far siltier than is usually tolerated by *N. hombergi* and no worms were found in this part of the beach. The substratum over the whole beach, though very silty, is poorly sorted and the presence of a large proportion of coarse particles apparently renders it barely tolerable for *N. cirrosa* in the sandier areas.

There is no evidence that tidal level plays any part in determining the distribution of *Nephtys* on this beach; and the distribution of almost all the other members of fauna is dominated by the variable nature of the substratum.

(*e*) *Kames Bay, Cumbrae, Scotland*

Although this bay is outside the area considered in this survey, it is of particular interest because the distribution of both intertidal and the sublittoral fauna has been studied in some detail (Stephen 1929, Watkin 1942, Clark & Milne 1955). *N. cirrosa* occurs intertidally and *N. hombergi* replaces it in the sublittoral. There has been an unfortunate confusion in the literature over the identity of the intertidal species of *Nephtys*. Stephen (1929) identified it as *N. caeca* but one of us (R. B. C.), through the courtesy of Dr Stephen, has been able to examine his specimens and found them to be *N. cirrosa*. Watkin (1942) was guided by Stephen in his identification of polychaetes and also erroneously recorded *N. caeca*. Repeated examination of *Nephtys* from Kames Bay since 1948 has shown the intertidal population to be almost exclusively *N. cirrosa* (Clark 1960).

Descriptions, maps and photographs of Kames Bay have previously been published by Stephen (1929), Watkin (1942), Smith (1955) and Clark & Milne (1955). The bay faces south-east and is sheltered from all other directions. The substratum is of clean sand, grade analyses of which at a number of stations between high and low water marks were made by Watkin (1942). It is not possible to make a direct comparison between Watkin's figures and our own because of the great difference in the series of sieves used, but the substratum at all stations in Kames Bay contains between 95·4 and 90·5% coarse particles (>0·2 mm). The silt and clay fraction is negligible over the whole tidal range, but the fine sand fraction (2·0-0·2 mm) becomes appreciable (about 10%) towards low water mark (Watkin 1942). There are no comparable data for the composition of the substratum in the sublittoral deposits. However, the trend towards finer substrata in the lower part of the beach continues and at the deepest station examined, at 27 m, the substratum is of mud (Clark & Milne 1955).

N. cirrosa is abundant in the intertidal zone. It first appears a little below

H W N (Fig. 6), and below mean sea level its density rapidly increases, reaching a maximum of about 50/m² at about L W N (Watkin 1942). Stephen (1929) reported a maximum density of 27/m², but found a similar distribution. This species has not been found below L W S, where its place is taken by *N. hombergi*. There is a narrow zone of overlap between L W N and L W S, where occasionally large specimens of *N. hombergi* are found with the much more numerous *N. cirrosa*. Clarke & Milne (1955) recorded *N. hombergi* from seven stations at depths between 1 and 27 m below L W O T, with relative densities ranging between nineteen and ninety-two specimens per sample of about 8000 ml of substratum (unfortunately this figure is not convertible to numbers per m²). The densities fluctuate from station to station and show no obvious relation to increasing depth. *N. hombergi* is widely distributed in sublittoral deposits of muddy sand throughout the Clyde area down to a depth of 80 m (Clark 1960). It does not occur at greater depths

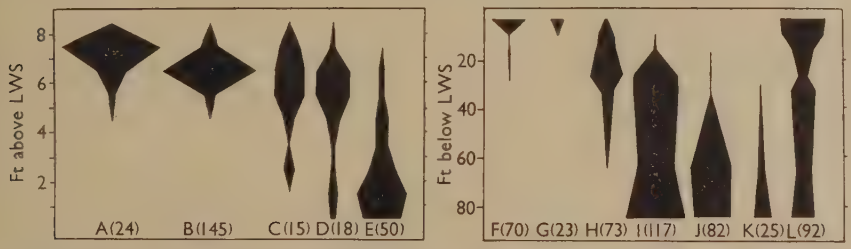


Fig. 6. Intertidal and sublittoral distribution of the commonest polychaetes at Kames Bay, Millport. Intertidal species: A, *Nerine cirratulus*; B, *Ophelia rathkei*; C, *Arenicola marina*; D, *Eteone flava*; E, *Nephtys cirrosa*. The figure at the foot of each polygon represents the maximum average density (number per m²) of that species in the transect. (Data extracted from Watkin 1942).

Sublittoral species: F, *Spio filicornis*; G, *Phyllodoce maculata*; H, *Sigalion mathildae*; I, *Owenia fusiformis*; J, *Goniada maculata*; K, *Glycera rouxi*; L, *Nephtys hombergi*. The figure at the foot of each polygon represents the maximum relative density of that species in the transect. (Data extracted from Clark & Milne 1955).

than this, where the substratum is generally of very fine mud composed entirely of particles less than 0·02 mm diameter (Allen 1954).

DISCUSSION

Previous investigators have sometimes characterized substrata by some sort of weighted average of the grade fractions (Allen 1899, Borley 1923, Holme 1954) but, quite apart from the inherent disadvantages of this method (Holme 1954, Morgans 1956), it is clearly too crude to distinguish between beaches occupied by species of *Nephtys*. Krumbein (1934, 1936, 1939) developed the use of a graphical presentation of cumulative grade fractions on a logarithmic scale (the φ scale), which Morgans (1956) has urged on marine ecologists. The advantage of this method of presenting analyses is that one may readily determine the median diameter of the particles in the sample, the degree of sorting and various other parameters. Some extreme data, extracted from Tables 2 and 3, are shown in this form in Fig. 7, and it is clear that the degree of sorting of the substrata is high on all the beaches, that there is not a very great variation in the median diameter of the particles,

but also that this technique is rather insensitive for distinguishing substrata for biological purposes. Within the limits of accuracy of this method, the median particle size (M) and degree of sorting of the substrata (phi quartile deviation, QD_ϕ) on the beaches containing *N. cirrosa*, *N. hombergi*, both species or neither, support the conclusions based on a more detailed consideration of the substratum analyses. While substrata occupied by *N. hombergi* are generally composed of finer material than those populated by *N. cirrosa*, the extreme range of substrata suitable for the former species overlaps the range suitable for the latter, and indeed both species occur together on a few beaches. The differences between substrata on beaches with different faunas are often subtle, and it is evident from the previous discussion of the substratum analyses that small variations in the

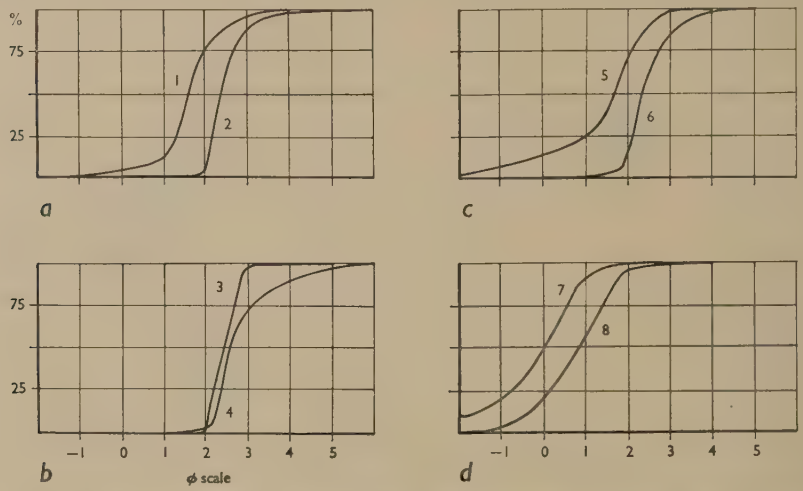


Fig. 7. Cumulative percentages of grade fractions, plotted on a logarithmic (Φ) scale, of substrata from a variety of beaches populated: *a*, by *Nephtys cirrosa*—1, Combe Martin (M = 0·32 mm, $QD\phi$ = 0·35), 2, Minehead 1 (M = 0·19 mm, $QD\phi$ = 0·24); *b*, by *N. hombergi*—3, Portishead (M = 0·19 mm, $QD\phi$ = 0·22), 4, Brean (M = 0·16 mm, $QD\phi$ = 0·36); *c*, by both species –5, Langstone Rock (M = 0·30 mm, $QD\phi$ = 0·50), 6, Seaton Beach (M = 0·20 mm, $QD\phi$ = 0·31); *d*, by neither species—7, Lynmouth (M = 1·00 mm, $QD\phi$ = 0·65), 8, Sillery (M = 0·56 mm, $QD\phi$ = 0·68). (Data extracted from Table 2.)

amount of coarse material or in the silt content have a critical effect on the fauna, a fact also noted by Holme (1954) in his study of the distribution of *Ensis*. Our attention is therefore directed to the coarsest and finest fractions in the substratum, even though the accuracy with which these can be determined may be limited by sampling errors (Morgans 1956).

Substrata populated by *Nephtys hombergi* but not by *N. cirrosa* contain more than 2-3% fine particles and sometimes as much as 34%, but include very little coarse material. *N. cirrosa* is generally found on beaches with less than 1·8% fine material and will tolerate 50% or more coarse material. Coarser beaches than this may contain a few *N. cirrosa*, but more often they have none, particularly if the coarser fractions in the substratum are composed of shell fragments. This species

will also tolerate relatively silty substrata, provided there is an admixture of coarse particles with the fine (*i.e.* if the substratum is relatively poorly sorted), and the presence of as little as 3-4 % coarse material may render an otherwise fairly silty substratum suitable for a dense population of the worm. This results in its range overlapping that of *N. hombergi* and so both species occur on a number of beaches with poorly sorted substrata. When such beaches are relatively coarse, as at Seaton Beach and Torquay, *N. cirrosa* predominates; when they are relatively fine, as at Dale and on the inner side of Dawlish Warren, *N. hombergi* is the more numerous species.

Except for the exposed sandy beaches of the north coast of Devon and Cornwall and a few other places, most of the marine beaches have substrata which are suitable for *N. cirrosa* but too coarse for *N. hombergi*. Silty beaches, suitable for *N. hombergi* but too fine for *N. cirrosa* are usually found only in the lower reaches of estuaries, and for this reason an examination of intertidal faunas gives the impression that *N. hombergi* is an estuarine species. This is a false impression, because such silty substrata are common in the sublittoral zone, where *N. hombergi* is relatively abundant in water of moderate depths (Clark & Milne 1955), whereas substrata suitable for *N. cirrosa* are probably a rarity in the sublittoral, to judge from the distribution of this species in Kames Bay, and from the fact that it has not often been recorded from sublittoral deposits (Caspers 1939, Southward 1957). It is quite likely that *N. hombergi* lives in the sublittoral zone of many of the beaches we have examined and this may account for the occurrence of a few large specimens near L W M at Marazion and Kames Bay, which are otherwise populated by *N. cirrosa* and appear to be more suitable for that species.

Both species of *Nephtys*, on beaches where they are all numerous, occupy a fairly well defined place in the intertidal zonation of animals (Figs. 2, 3 and 6). As a rule they occur between mean tide level and low-water mark, with a maximum density in the lowest part of the zone occupied by *Arenicola* though *Nephtys cirrosa* tends to occur in greatest numbers rather lower down the beach than *N. hombergi*. The factors that govern the intertidal zonation of animals on sandy beaches are complex and generally less obvious than those on rocky shores; they have been discussed in recent years by Yonge (1949, 1950). Some detritus- and suspension-feeding lamellibranchs are limited in their intertidal distribution by the length of time feeding is interrupted by the recession of the tide (Yonge 1949), but the distribution of most burrowing animals depends not upon tidal exposure, but upon the composition of the substratum in one way or another. This appears to be true at least of *N. hombergi*, which is not always confined to the lower half of the beach, but may occur near H W N, if a suitable substratum is available there (as at Stolford and Dale), or be restricted to the region between L W N and L W S (as at Kames Bay), if the higher levels on the beach consist of coarse sand. We have less information about the intertidal distribution of *N. cirrosa*, but at Dale it is scattered at all tidal levels, suggesting that it too is limited in its distribution on the beach by the composition of the substratum rather than by tidal exposure.

The grade composition determines the physical properties of a substratum and

these are often the ultimate determinants of the fauna of sandy and muddy beaches. We have refrained from speculating upon which of many physical factors might be related to the distribution of *Nephtys*, because this subject is at present under investigation and we hope to consider it in a later paper.

ACKNOWLEDGMENTS

We are particularly indebted to Mr R. Bassindale for his advice and assistance in many ways during the course of this investigation. Prof. E. W. Knight-Jones kindly made some preliminary collections of *Nephtys* for us at Swansea and the Mumbles. The survey of the distribution of *Nephtys* at Dale was made possible by the efforts of a party of students from the Zoology Department, University of Bristol, and the Haverfordwest R.D.C. kindly made available the results of their levelling survey of the Gann Flats. One of us (E. C. H.) held a National Science Foundation Science Faculty Fellowship while on sabbatical leave from Monterey Peninsular College, Monterey, California, and is also happy to acknowledge the hospitality and facilities placed at his disposal at the Plymouth Laboratory, where part of the work was done.

SUMMARY

1. Around the coasts of south and south-western England and South Wales, *N. cirrosa* occurs on most clean, sandy beaches of the open coast, except in north Cornwall and Devon, where the beaches are exposed and the substratum is coarse. *N. hombergi* is found in estuarine or semi-estuarine conditions in the Bristol Channel and the Tamar and Exe estuaries, and in the sheltered but essentially marine beaches at Dale and in the Salcombe estuary.

2. The limit of penetration of *N. hombergi* into estuaries is the point at which tidal salinity fluctuations, particularly in winter, are severe.

3. The occurrence of one or other species on a beach can be correlated with the grade composition of the substratum.

4. *N. hombergi* occurs in greatest numbers in a substratum containing 0·3% particles greater than 0·25 mm diameter and 5·8% particles smaller than 0·125 mm diameter. The optimum substratum for *N. cirrosa* contains between 4 and 7% particles larger than 0·25 mm and about 1·8% smaller than 0·125 mm.

5. *N. hombergi* tolerates up to 3·8% particles greater than 0·25 mm and between 2·2 and 15·9% particles smaller than 0·125 mm. *N. cirrosa* tolerates up to 50% particles larger than 0·25 mm; coarser substrata may be colonized unless the larger grades are composed of shell fragments; it will also tolerate more than 1·8% fine particles, providing the substratum also includes a proportion of coarse particles.

6. Beaches composed of poorly sorted substrata containing relatively large proportions of coarse and fine material may be colonized by both species; they form a small minority of those investigated.

7. Where they are numerous, *N. cirrosa* and *N. hombergi* generally occur below M T L, but are not restricted to a particular tidal zone. Their distribution on a beach is determined largely by the composition of the substratum.

8. *N. hombergi* is principally sublittoral and occurs intertidally only in the lower reaches of estuaries or on extremely sheltered beaches. Substrata suitable for *N. cirrosa* are rare in the sublittoral but usual on all but the most exposed marine sandy beaches; it is therefore the predominant species around the south and west coasts of Britain.

REFERENCES

Allen, E. J. (**1899**). On the fauna and bottom-deposits near the thirty-fathom line from the Eddystone Grounds to Start Point. *J. Mar. Biol. Ass. U.K.* **5,** 365-542.

Allen, E. J. & Todd, R. A. (**1900**). The fauna of the Salcombe estuary. *J. Mar. Biol. Ass. U.K.* **6,** 151-217.

Allen, E. J. & Todd, R. A. (**1902**). The fauna of the Exe estuary. *J. Mar. Biol. Ass. U.K.* **6,** 295-343.

Allen, J. A. (**1954**). A comparative study of the British species of *Nucula* and *Nuculana*. *J. Mar. Biol. Ass. U.K.* **33,** 457-72.

Bassindale, R. (**1938**). The intertidal fauna of the Mersey estuary. *J. Mar. Biol. Ass. U.K.* **23,** 83-98.

Bassindale, R. (**1940**). Studies on the biology of the Bristol Channel. IV. The invertebrate fauna of the southern shores of the Bristol Channel and Severn estuary. *Proc. Bristol Nat. Soc.* (4), **9,** 143-201.

Bassindale, R. (**1943a**). A comparison of the varying salinity conditions of the Tees and Severn estuaries. *J. Anim. Ecol.* **12,** 1-10.

Bassindale, R. (**1943b**). Studies on the biology of the Bristol Channel. XI. The physical environment and intertidal fauna of the southern shores of the Bristol Channel and Severn estuary. *J. Ecol.* **31,** 1-29.

Bassindale, R. & Barrett, J. H. (**1957**). The Dale Fort marine fauna. *Proc. Bristol Nat. Soc.* **29,** 227-328.

Beanland, F. L. (**1940**). Sand and mud communities in the Dovey estuary. *J. Mar. Biol. Ass. U.K.* **24,** 589-611.

Borley, J. O. (**1923**). The marine deposits of the southern North Sea. *Fish. Invest.* (II), **4,** No. 6.

Caspers, H. (**1939**). Der Bodenfauna der Helgoländer Tiefen Rinne. *Helgoland wiss. Meeresunters.* **2,** 1-112.

Clark, R. B. (**1960**). *Fauna of the Clyde Sea Area. Polychaeta.* Millport.

Clark, R. B. & Milne, A. (**1955**). The sublittoral fauna of two sandy bays on the Isle of , Cumbrae, Firth of Clyde. *J. Mar. Biol. Ass. U.K.* **34,** 161-80.

Coleman, J. (**1940**). On the faunas inhabiting intertidal seaweeds. *J. Mar. Biol. Ass. U.K.* **24,** 129-83.

Crisp, D. J. & Southward, A. J. (**1958**). The distribution of intertidal organisms along the coasts of the English Channel. *J. Mar. Biol. Ass. U.K.* **37,** 157-208.

Elwes, E. V. (**1909**). Notes on the littoral polychaeta of Torquay. Part II. *J. Mar. Biol. Ass. U.K.* **8,** 347-58.

Haderlie, E. C. & Clark, R. B. (**1959**). Studies on the biology of the Bristol Channel. XIX. Notes on the intertidal fauna of some sandy and muddy beaches in the Bristol Channel and Severn estuary. *Proc. Bristol Nat. Soc.* **29,** 459-68.

Hartman, O. (**1950**). Goniadidae, Glyceridae and Nephtyidae. *Allan Hancock Pacif. Exped.* **15,** 1-181.

Hartman, O. (**1954**). Polychaeta, in **Light S. L.,** et al. *Marine invertebrates of the central Californian coast.* Berkeley.

Harvey, H. W. (**1945**). *Recent advances in the chemistry and biology of sea water.* Cambridge.

Holme, N. A. (**1949**). The fauna and sand and mud banks near the mouth of the Exe estuary. *J. Mar. Biol. Ass. U.K.* **28,** 189-237.

Holme, N. A. (**1954**). The ecology of British species of *Ensis*. *J. Mar. Biol. Ass. U.K.* **33,** 145-72.

Krumbein, W. C. (**1934**). Size frequency distribution of sediments. *J. Sediment. Petrol.* **4,** 65-77.

Krumbein, W. C. (**1936**). Application of logarithmic moments to size frequency distributions of sediments. *J. Sediment. Petrol.* **6,** 35-47.

Krumbein, W. C. (**1939**). Graphic presentation and statistical analysis of sedimentary data, pp. 558-91 in **Trask, P. D.** (ed.). *Recent Marine Sediments: a symposium.* Tulsa.

Marine Biological Association (**1957**). *Plymouth Marine Fauna.* Plymouth.

Milne, A. (1938). The ecology of the Tamar estuary. III. Salinity and temperature conditions in the lower estuary. *J. Mar. Biol. Ass. U.K.* **22,** 529-42.

Morgans, J. F. C. (1956). Notes on the analysis of shallow-water soft substrata. *J. Anim. Ecol.* **25,** 367-87.

Percival, E. (1929). A report on the fauna of the estuaries of the River Tamar and the River Lynher. *J. Mar. Biol. Ass. U.K.* **16,** 81-108.

Purchon, R. D. (1937). Studies on the biology of the Bristol Channel. II. An ecological study of the beach and dock at Portishead. *Proc. Bristol Nat. Soc.* (4), **8,** 311-29.

Purchon, R. D. (1947). Studies on the biology of the Bristol Channel. XVII. The littoral and sub-littoral fauna of the northern shores near Cardiff. *Proc. Bristol Nat. Soc.* **27,** 285-310.

Purchon, R. D. (1956). Studies on the biology of the Bristol Channel. XVIII. The marine fauna at five stations on the northern shores of the Bristol Channel and Severn estuary. *Proc. Bristol Nat. Soc.* **29,** 213-26.

Rees, C. B. (1940). A preliminary study of the ecology of a mud-flat. *J. Mar. Biol. Ass. U.K.* **24,** 185-199.

Reid, J. M. (1930). On some factors limiting the habitat of *Arenicola marina*. *J. Mar. Biol. Ass. U.K.* **16,** 109-99.

Smith, R. I. (1955). Salinity variation in interstitial water of sand at Kames Bay, Millport, with reference to the distribution of *Nereis diversicolor*. *J. Mar. Biol. Ass. U.K.* **34,** 33-46.

Smith, R. I. (1956). The ecology of the Tamar estuary. VII. Observations on the interstitial salinity of intertidal muds in the estuarine habitat of *Nereis diversicolor*. *J. Mar. Biol. Ass. U.K.* **35,** 81-104.

Southward, E. C. (1957). The distribution of polychaeta in offshore deposits in the Irish Sea. *J. Mar. Biol. Ass. U.K.* **36,** 49-75.

Spooner, G. M. & Moore, H. B. (1940). The ecology of the Tamar estuary. VI. An account of the macrofauna of the intertidal muds. *J. Mar. Biol. Ass. U.K.* **24,** 283-330.

Stephen, A. C. (1929). Studies on the Scottish marine fauna: the fauna of the sandy and muddy areas of the tidal zone. *Trans. Roy. Soc. Edin.* **56,** 291-306.

Watkin, E. E. (1942). The macrofauna of the intertidal sand of Kames Bay, Millport, Buteshire. *Trans. Roy. Soc. Edin.* **60,** 543-61.

Webb, J. E. (1958). The ecology of Lagos lagoon. V. Some physical properties of lagoon deposits. *Philos. Trans. Roy. Soc.* **241,** 307-419.

Wentworth, C. K. (1922). A scale of grade and class terms for clastic sediments. *J. Geol.* **30,** 377-92.

Wilson, D. P. (1949). The decline of *Zostera marina* L. at Salcombe and its effects on the shore. *J. Mar. Biol. Ass. U.K.* **28,** 395-412.

Yonge, C. M. (1949). *The sea shore.* London.

Yonge, C. M. (1950). Life on sandy shores. *Sci. Progr.* No. 151, 430-44.

APPENDIX

BEACHES EXAMINED IN THE FAUNISTIC SURVEY

(The national grid number follows in parentheses the name of each collecting ground.)

1. Gann Flats, Dale, Pembrokeshire (SM 815065). *Nephtys hombergi* present in moderate numbers, *N. cirrosa* present, but rare (see p. 132).

2. Pendine, Carmarthenshire (SN 234078). Shingle at H W M below sea-wall. The rest of the beach composed of very firm sand containing many shell fragments. Some fresh-water running across the beach. *Arenicola marina* common. No *Nephtys* found. Salinity 28·0‰.

3. The Mumbles, Swansea Bay, Glamorganshire (SS 626877). Shingle bank at H W M. The rest of the beach composed of sand lying on clay. *N. cirrosa*. Salinity 26·3‰.

4. Swansea, Glamorganshire (SS 635915). Sand dunes at H W M above a flat, sandy beach. Extensive *Arenicola* beds. Both *Nephtys cirrosa* and *N. hombergi* present. Salinity 26·4‰.

5. Port Talbot, Glamorganshire (SS 745888). Beach exposed to heavy surf, composed of clean sand with numerous shell fragments. Some fresh-water running across the beach. *Haustorius arenarius* (Amphipoda) present. *Nephtys cirrosa* fairly common around and below M T L. One *N. longosetosa* found above M T L. Salinity 30·8‰.

6. Porthcawl, Glamorganshire (SS 823765). Beach exposed to heavy surf. Shingle bank near the sea-wall, the rest of the beach composed of clean sand containing pebbles and shell fragments. *Nerine cirratulus* common. *Nephtys cirrosa* fairly common at M T L. Salinity 29·8‰.

7. Llantwit Major, Glamorganshire (SS 956673). Cliffs at H W M, beach strewn with boulders, with clean sand between them. A considerable amount of fresh-water runs across the beach. Intertidal fauna, chiefly of the rocks, described by Purchon (1956). Purchon found one *N. caeca* in the sand, but after extensive search we found only *N. cirrosa* in a few scattered areas about M T L. Salinity 30·0‰.

8. Limpert Bay, Glamorganshire (ST 020660). Shingle bank at H W M, the rest of the beach composed of large boulders with areas of sand between them; becoming muddy towards L W M. *Phyllodoce mucosa* and *Scoloplos armiger* fairly common. *Nephtys cirrosa* in dark sand at about M T L. Salinity 27·2‰.

9. Sully, Glamorganshire (between the mainland and Sully Island) (ST 169673). Beach composed of coarse shingle and gravel, with small, scattered patches of sand. Mud deposited on the sand, particularly towards L W M. Fauna described by Purchon (1948). *Arenicola marina* in the sandy patches. No *Nephtys* found.

10. Peterstone Wentlooge, Monmouthshire (ST 272795). Bed of *Spartina* between H W S and H W N, the rest of the beach composed of estuarine mudflats containing numerous *Nereis diversicolor*, *Macoma balthica* and *Hydrobia ulvae*. Fauna described by Rees (1940) and Purchon (1948). Rees reported finding *Nephtys* sp., but none was found in the present survey.

11. Portskewett, Monmouthshire (ST 515882). Estuarine mudflats, densely populated by *Nereis diversicolor*. Boulders lying on the mud in some places, fauna described by Purchon (1956). No *Nephtys* found.

12. Aust, Gloucestershire (ST 565897). Estuarine mud flats at the foot of Aust cliff; some rock and debris from the cliff occupy the upper part of the beach and algae grow on some of the rocks lying in the mud. The mud is very thick and is populated by *Nereis diversicolor*. No *Nephtys* found. Salinity 13·2‰.

13. Sugarhole Sands, Gloucestershire (ST 544865). Estuarine mudflats with a shingle bank at the top of the beach. A small freshwater stream flows across the mudflats upstream from the collecting area. Mud populated by *Nereis diversicolor*. No *Nephtys* found. Salinity 5·3‰ (reduced by local influence of the stream).

14. Royal Beach, Portishead, Somerset (ST 470777). Upper half of the beach composed of boulders and rocks with pebble and shingle at the foot of a low cliff. Areas of soft mud between the rocks, and the lower half of the beach is exposed to strong currents and consists of 15 cm clean sand lying on hard clay. The upper half of the beach has a covering of algae and has a limited fauna (described by Purchon 1937). *Nereis diversicolor* occurs in the pockets of mud between the rocks. The sand contains a small number of *Nephtys hombergi* near L W M.

15. Kilkenny Bay, Portishead, Somerset (ST 465775). At H W M there is a shingle bank running down to large stones lying on thick mud. The beach is protected from currents by a small headland separating it from Royal Beach and the upper half of it is composed of thin, sticky mud, 20–25 cm deep, lying on clay. Below M T L, this is replaced by laminated hard compacted mud alternating with sand. A layer of sand up to 5 cm thick lies on the surface in summer, mud is deposited on the beach in winter. Drainage runnels from the shingle bank cross the upper half of the beach. Mud contains numerous *Nereis diversicolor*. The sand below M T L contains some *Macoma balthica* and a few *Nephtys hombergi*. Salinity 21·2‰.

16. Clevedon, Somerset (ST 400718). A number of reefs run across the beach perpendicular to the shore. These are covered with algae. Fauna of the rocks included in Bassindale (1940). The areas between the reefs are filled with thin, sticky mud and contain no animals. There is a narrow zone of gravel immediately below the sea-wall at H W M, also without a macrofauna. No *Nephtys* found. Salinity 21·2‰.

17. Weston-super-Mare, Somerset (ST 315613). The upper half of the beach composed of sand lying on clay. In the lower half of the beach, slimy mud covers the sand to an increasing depth and eventually replaces it at L W M. Fauna of the sand includes *Arenicola marina*, *Macoma balthica* and a few *Corophium volutator* at M T L. *Nephtys hombergi* is common in the sand at the lower level reached by *Arenicola*. Salinity 23·7‰.

18. Brean, Somerset (ST 295575). *Nephtys hombergi* abundant (see p. 129). Salinity 23·8‰.

19. Steart, Somerset (ST 263475). A dense growth of *Spartina* extends from H W S to H W N. Below this, estuarine mudflats dissected by drainage runnels are exposed for a distance of about 3 miles at low water. At the edge of the *Spartina* belt there are small patches of sand lying on black mud. The mudflats are densely and almost exclusively populated by *Nereis diversicolor*. No *Nephtys* found in the sand or mud. Salinity 25·06‰.

20. Stolford, Somerset (ST 235460). A vast area of mudflats similar to those at Stolford and continuous with them, exposed at low tide. Populated by *Nereis diversicolor*. Upper part of the beach consists of a shingle bank at H W S and a region of pebble and rock lying on coarse sand and gravel, varying between 50 and 100 m in width, below the shingle bank. Small patches of sand lying on black mud at the junction between this zone and the mudflats. These patches of sand contain *Nereis diversicolor*, *Arenicola marina* and *Nephtys hombergi* in small numbers. Salinity 25·1‰.

21. Blue Anchor, Somerset (ST 032438 and 022438). Shingle and coarse sand at H W M. The upper half of the beach is composed of clean sand, but below M T L thin slimy mud covers the sand to an increasing depth. Fauna, mainly of the neighbouring rocky areas, included in Bassindale (1940). *Arenicolor marina* common over the upper half of the beach to M T L. *Nephtys cirrosa* abundant at M T L. Salinity 29·4‰.

22. Minehead, Somerset (SS 986467) (see p. 129). *N. cirrosa* common. Salinity 28·4‰.

23. Sillery Sands, Lynmouth Bay, Devon (SS 741498). Upper half of the beach composed of rock, boulders, shingle and gravel lying at the foot of a cliff. Narrow sandy beach below M T L. Streams of fresh-water from the cliff run across the sand. Rocks with a slight algal growth and rock fauna included in Bassindale (1940). No animals in the sand. Salinity 33·6‰.

24. Lynmouth Harbour, Devon (SS 725498). Slate fragments and shingle form the upper half of the beach. Below M T L there are patches of coarse sand 5-10 cm deep

lying on rock. River Lyn flows into the sea ¼ mile west of the collecting area. Fauna of rocky areas included in Bassindale (1940). No *Nephtys* found. Salinity 30·6‰.

25. Combe Martin, Devon (SS 573473). Shale outcrops form reefs running across the beach from H W S. Spaces between them are filled with boulders in the upper half of the beach, with sand in the lower half. River Umber flows across the beach in a well-defined channel and there is a considerable amount of fresh-water running over the beach, disappearing into the sand. Reefs bear a dense algal growth and support a typical rock fauna. In the sand below M T L there are small beds of *Arenicola marina* chiefly where the fresh-water drains into the sand. Elsewhere *Scolelepis fuliginosa* is common. *Nephtys cirrosa* fairly common in association with *Scolelepis*. Salinity 21·9‰.

26. Ilfracombe, Devon (SS 518479). Slate reefs run across the beach, areas between them are filled with sand. Exposure to wave action is severe and there are no algae on the rocks. The rock fauna is mainly in crevices and is included in Bassindale (1940). No *Nephtys* found. Salinity 35·0‰.

27. Woolacombe Sands, Morte Bay, Devon (SS 454435). Flat, sandy beach ¼ mile wide at low water. Sand dunes above H W S. Stream of fresh-water runs across the beach and drains into the sand. One *Portumnus latipes* (Decapoda) found after extensive digging. No *Nephtys* found. Salinity 33·2‰.

28. Croyde Bay, Devon (SS 433394). Low cliffs at the top of the beach which is composed of clean sand. Rocky reefs covered with algae and supporting a typical rock fauna run through the sand immediately north of the collecting area. A few *Haustorius arenarius* (Amphipoda) found in the sand. No *Nephtys* found. Salinity 33·5‰.

29. Instow, Devon (SS 472311). Clean, firm sandy beach at the junction of River Taw and River Torridge. A few *Arenicola marina* and *Nereis diversicolor*. No *Nephtys* found. Salinity 23·7‰.

30. Westward Ho!, Devon (SS 432925). Shingle bank at H W M above a clean sandy beach. Exposed to severe wave action and heavy littoral drift. No *Nephtys* found. Salinity 34·5‰.

31. Bude, Cornwall (SS 200070). Sheer cliffs at the back of a beach composed of clean sand with rock reefs running across it nearly to L W M. A considerable amount of fresh-water running across the beach. Beach exposed to heavy surf action. Large and varied fauna on the reefs including *Mytilus* beds and massive colonies of *Sabellaria alveolata*. *Ammodytes* sp. in sand. No *Nephtys* found. Salinity 33·5‰.

32. Pentireglaze, Cornwall (SW 934795). Clean sandy beach at the foot of low cliffs, broken by reefs running from H W M. Considerable amount of fresh-water running across the beach. Rocks covered with algae and support a varied fauna. *Haustorius arenarius* (Amphipoda), *Portumnus latipes* (Decapoda), *Nerine cirratulus* and nemerteans common in the sand. A belt of *Arenicola marina* from M T L to L W N. *Nephtys cirrosa* common near L W M, but not found elsewhere on the beach. Salinity 34·4‰.

33. Newquay Bay, Newquay, Cornwall (SW 815620). Clean sandy beach at the foot of cliffs, with rocky reefs. No *Nephtys* found. Salinity 35·0‰.

34. Fistral Bay, Newquay, Cornwall (SW 798623). Similar to Newquay Bay, but with sand dunes above H W M. Heavy surf. Fauna of sand very sparse. One *Portumnus latipes* (Decapoda) and two *Nephtys cirrosa* found after extensive digging. Salinity 35·0‰.

35. Perranporth, Cornwall (SW 756547). Clean sandy beach with sand dunes and cliffs at H W M. Some rocky reefs running across the beach covered with algae and supporting a typical rock fauna. A fresh-water stream crosses the beach in a well-defined channel. Fauna of the sand sparse. Two *N. cirrosa* found a little below M T L after extensive digging. Salinity 31·3‰.

36. Carbis Bay, Cornwall (SW 530388). Exposed sandy beach at the foot of cliffs. Some fresh-water running over the sand. One *Nerine foliosa* and one *Nephtys cirrosa* found after extensive digging. Salinity 29·4‰.

37. Sennen Cove, Cornwall (SW 355264). Large granite boulders at the foot of cliffs. Clean sand to L W M. Some fresh-water running across the beach. Rocks with algae and typical rock fauna (described by Crisp & Southward 1958). *Ammodytes* found in the sand. No *Nephtys* found. Salinity 35·0‰.

38. Marazion, Cornwall (SW 515307). Shingle bank at H W M, clean sand to L W M, dissected by occasional rocky reefs covered with algae and rock fauna (Crisp & Southward 1958). *Arenicola marina* common in the sand at M T L. *Glycera* sp. in the lower part of the beach. *Nephtys cirrosa* and *N. hombergi* almost equally abundant over the whole of the beach, though with a slight preponderance of *N. cirrosa*. Salinity 32·6‰.

39. Prah Sands, Cornwall (SW 575280). Sand dunes above H W M. Beach composed of clean sand with a considerable volume of fresh-water running across it. No *Nephtys* found. Salinity 32·7‰.

40. Porthleven, Cornwall (SW 628253). Shingle bank at H W M, the rest of the beach composed of gravelly sand. No *Nephtys* found. Salinity 32·5‰.

41. Maen Porth, Falmouth Bay, Cornwall (SW 791297). Shingle bank at H W M, rest of the beach composed of muddy sand with occasional boulders. Protected from wave action, with a considerable volume of fresh-water running across the sand. Rock fauna described by Crisp & Southward (1958). Sand contains *Arenicola marina* at M T L. *Lanice conchilega*, *Nerine cirratulus*, *Ensis arcuata* and *Tellina tenuis* moderately common in lower half of the beach. *Nephtys cirrosa* very common. Salinity 4·5‰.

42. Porthluney Cove, Veryan Bay, Cornwall (SW 974412). Shingle bank at H W M, beach composed of sand with a few pebbles. Well protected and with a small freshwater stream running across the sand. Two *N. cirrosa* found. Salinity 27·6‰.

43. Par, Cornwall (SX 085530). Beach composed of fine sand with a considerable deposition of china clay, carried in by streams. *Nerine cirratulus* and two *Nephtys cirrosa* found. Salinity 21·9‰.

44. Seaton Beach, Cornwall (SX 302543). Small sandy beach bounded on either side by rocky cliffs. Shingle at the foot of the cliff at H W M, fresh-water seeping from the foot of the cliff runs across the sand. *Arenicola marina* common from the edge of the shingle to L W M. *Nerine cirratulus*, *Audouinia tentaculata* and *Glycera* sp. also present. *Nephtys cirrosa* abundant from a little above M T L to L W M, a few large *N. hombergi* near L W M. Salinity 31·5‰.

45. Whitesand Bay, Cornwall (SX 414505). Beach of clean sand running from the foot of cliffs to L W M. Several reefs cross the beach to the east of the collecting area. Rock fauna described by Crisp & Southward (1958). Moderately exposed to wave action. *Glycera* sp. present. *Nephtys cirrosa* moderately common.

46. Tamar estuary. Surveyed by Spooner & Moore (1940) and Smith (1956). Not reinvestigated in the present survey. Intertidal mudflats inhabited by *Nereis diversicolor* etc. *Nephtys hombergi* reported from St John's Lake to Wierquay. Salinity data in Milne (1938).

47. Wembury, Devon (SX 516483). Cliffs at H W M with shingle and shale at the highest levels on the beach, remainder composed of sand with reefs running seawards on either side of the collecting area. Freshwater stream crosses the beach. Rock fauna described by Colman (1940) and others. Sand contains numerous *Nerine cirratulus*, *Scolelepis fuliginosa*. No *Nephtys* found. Salinity 17.7‰.

48. Bigbury-on-Sea, Devon (SX 653442). Shale at H W M, with reefs running across the beach to L W M. Sand between the reefs. *Nerine cirratulus* present. Some *Nephtys cirrosa* in the sand. Salinity 27·5‰.

49. Salcombe, Devon (SX 732381). Small sandy beach at the seaward end of the harbour. *Arenicola* at M T L. *Nerine cirratulus* and *Goniada maculata* also present. Some *Nephtys cirrosa* and two large *N. hombergi* found in the lower half of beach. Salinity 34·0‰.

50. East Portlemouth, Devon (SX 744388). Low cliffs at H W M, clean sandy beach

subject to erosion in the lower part of the harbour with a deposition of sand at Ditch End Corner (see Wilson 1949). No *Nephtys* found. Salinity 33·9‰.

51. Upper Salcombe estuary. Surveyed by Allen & Todd (1900). Not reinvestigated in the present survey. *N. hombergi* reported from mouth to Garston Point.

52. Paignton, Devon (SX 895610). Pebble and sand at H W M, the rest of the beach composed of clean sand. Some fresh-water running across the beach. Sand sparsely populated. *Nerine cirratulus* and *Portumnus latipes* (Decapoda) present. *Nephtys cirrosa* moderately common at M T L. Salinity 35·0‰.

53. Tor Abbey Sands, Torquay, Devon (SX 911636). Both *N. cirrosa* and *N. hombergi* present in moderate numbers (see p. 131). Salinity 35·0‰.

54. Teignmouth, Devon (SX 942727). Beach composed of sand and gravel. A little fresh-water running over the beach. *N. cirrosa* in small numbers at M T L. Salinity 35·0‰.

55. Langstone Rock, Dawlish Warren, Devon (SX 981783). Fine sandy beach on the seaward side of Dawlish Warren. *Glycera convoluta, Magelona papillicornis, Nerine cirratulus* and *Aricia latreilli* present. A few *Nephtys cirrosa* and one large *N. hombergi* found. Salinity 35·0‰.

56. Lower Exe estuary, Dawlish Warren, Devon. Surveyed by Holme (1949). Not reinvestigated in the present survey. Protected beach on the inner side of Dawlish Warren, containing *N. hombergi* and *N. cirrosa*, the former more numerous. Salinity data in Holme (1949).

56a. Exe estuary, Devon. Surveyed by Allen & Todd (1902). Not reinvestigated in the present survey. *N. hombergi* reported on muddy sand banks from the mouth of the estuary to Powderham. Salinity data in Holme (1949).

57. Lyme Regis, Dorset (SY 339916). Most of the beach composed of shingle, but small areas of sand near the breakwater in Cobb Harbour. Considerable volume of fresh-water on the sand. *Arenicola marina, Scoloplos armiger* and *Lanice conchilega* present in the sand. Two *Nephtys cirrosa* found after extensive digging. Salinity 28·2‰.

58. Weymouth, Dorset (SY 681795). Pebble and sand near the sea-wall, rest of the beach composed of clean sand. Some *Arenicola marina* near M T L; *Sthenelais boa* and *Nerine cirratulus* in the upper half of the beach. No *Nephtys* found, but only the upper half of the beach investigated. Salinity 33·3‰.

A QUANTITATIVE STUDY OF THE PREDATORS ON THE EGGS AND LARVAE OF THE BROOM BEETLE, *PHYTODECTA OLIVACEA* FORSTER, USING THE PRECIPITIN TEST

By J. P. DEMPSTER

Imperial College, London

(With 4 Figures in the Text)

The Chrysomelid beetle (*Phytodecta olivacea* Forster) is common on broom (*Sarothamnus scoparius* L.) at Imperial College Field Station, Silwood Park, Ascot, Berks. Since 1954 a population of this beetle has been studied by Professor O. W. Richards and Dr N. Waloff, in an area of about 2 acres of broom. During the course of their work it became apparent that there was a large disappearance of the young stages of the beetle and that this disappearance coincided with the occurrence of large numbers of predacious insects, particularly Miridae, on the broom.

Since 1956 I have been studying these predators by means of the precipitin test. This test is based upon the interaction of *Phytodecta* material in the gut of a predator with antibodies in the blood serum of rabbits, which have been innoculated with an extract of the beetle. The precipitin test has been used previously by other workers to determine the predators of a number of prey. Brook & Proske (1946) studied the predators of mosquito larvae; Hall, Downe, MacLellan & West (1953) the predators of the eggs of tortricids and olethreutids and of the larvae of the forest tent caterpillar (*Malacosoma disstria* Hbn.); while Fox & MacLellan (1956) studied the carabids and staphylinids preying on the wireworm *Agriotes sputator* L. In all these cases, however, the test was used qualitatively to show what predators were feeding on the prey. An attempt is made here to make the results from the test quantitative and to estimate the effect of each predator on the *Phytodecta* population.

The life cycle of *Phytodecta* has been described by Waloff & Richards (1958), and may be summarized as follows. Overwintering, adult beetles emerge in April from the litter under the broom brushes where they have been hibernating. They feed on the broom and oviposit on the foliage. Egg-laying takes place throughout the summer until the end of August, by which time all of the adults have returned to the soil where they either die or hibernate until the next spring. There are four larval instars which all feed on the broom, the last one, when fully fed, entering the soil where pupation occurs. The pupae give rise to adults from August to October, and these feed on the broom before returning to the soil for hibernation. These adults are sexually immature and do not mate or oviposit until the following spring. Egg-laying takes place over a period of about 3 months so that all stages from egg to adult are to be found during most of the summer.

The predators considered here are those preying upon the eggs and larvae of

the beetle on the broom plant. There is some loss from predation of the pupae in the debris and soil under the bushes, but this is described elsewhere (Dempster, Richards & Waloff 1959).

MATERIALS AND METHODS

(*a*) *Preparation of antigen*

The procedure used for the preparation of a cell-free extract of *Phytodecta* is based on that described by Leone (1947). Adult beetles are starved for 3 days to remove broom from their guts, killed in a cyanide bottle and then crushed in a pestle and mortar with normal saline solution (0·9% NaCl). This is kept for 24 h at 4° C, centrifuged and then sterilized by passing it through a Seitz EK sterilizing filter pad. At the beginning of this work, the extract was spoilt by a deposition of melanin after filtering, but this was inhibited subsequently by the addition of M/1000 potassium cyanide to the crushed beetles. The clear, sterile antigen is freeze-dried and stored until sufficient has been accumulated.

(*b*) *Production of antiserum*

The *Phytodecta* antigen is reconstituted with distilled water and the soluble proteins precipitated with 0·4% potassium alum (Proom 1943). The pH of the resulting suspension is adjusted to 6·8, and 2·5 ml are injected intramuscularly into each hind leg of a rabbit. Ten to 14 days after inoculation the rabbit is bled from the ear and its serum tested against a standard *Phytodecta* extract. Further injections are given until the serum is sensitive enough. The production of antibodies varies somewhat between individual rabbits, but usually reaches a peak after the fourth or fifth injection, after which it falls off; 50 ml of blood is taken from each rabbit after the fourth and fifth injections. All sera which are sufficiently sensitive are pooled, sterilized, freeze-dried and stored. Lipoids must be removed from serum before freeze-drying or it becomes opaque when reconstituted with distilled water. This is done by a method described by McFarlane (1942), the lipoids being extracted with ether at a temperature below −25° C. All sera used in this work reacted with the standard *Phytodecta* extract diluted 1 : 8000; this represents a sensitivity to 1/20 000th part of an adult beetle in 0·02 ml of saline solution.

With successive injections the specificity of the serum decreases, that is, its reaction with insects other than *Phytodecta* increases. Again, there is some variation between individual rabbits, but the serum I have obtained reacts fairly strongly with other Chrysomelidae and Cassididae, and gives some reaction with Coccinellidae. Fortunately, the only chrysomelid on the broom is *Phytodecta*, and only the occasional stray from other plants is found. Only in the order of a dozen individuals of other Chrysomelidae and Cassididae have been found by Professor Richards and Dr Waloff in their weekly samples over 5 years. The Coccinellidae are, however, another matter, since they are fairly numerous and are not only possible predators of *Phytodecta*, but are possibly alternate prey to other predators.

The reaction to ladybirds is generally only about 1/400 as strong as that to *Phytodecta*, and can be neutralized by a technique known as absorption (Weitz 1952). This is done by adding just sufficient ladybird material to precipitate the antibodies to it. A slight excess of ladybird greatly reduces the sensitivity of the serum to *Phytodecta*. As far as my tests go, the reaction to all ladybirds can be removed by the addition of material from one species (*Coccinella septempunctata*).

Besides anti-*Phytodecta* serum, serum-containing antibodies to broom was also obtained, by the injection of rabbits with an extract of broom. Many of the predators being studied are omnivorous, and this serum was used to investigate the extent to which they were feeding on the host plant. The anti-broom serum reacted strongly with gorse, and although this reaction could be removed by absorption this considerably reduced the sensitivity of the serum.

(*c*) *Collection of predator meals*

A sample of the possible predators of *Phytodecta* is brought into the laboratory once or twice a week and identified to species and instar. Smears are made on filter paper of either the whole animal, in the case of small arthropods (Heteroptera, mites, etc.), or of just the gut contents (earwigs, beetles, etc.). These smears are labelled and dried rapidly over phosphorus pentoxide. Smears dried in this way have been stored for over 2 years without deteriorating.

(*d*) *The precipitin test*

For testing, the smears are cut from the filter paper and placed in 1 ml centrifuge tubes, with either 0·1 or 0·2 ml of normal saline solution, according to the size of the smear. Smears of mites and first- to third-stage nymphs of Miridae and Anthocoridae are extracted with 0·1 ml, and all others with 0·2 ml saline. The smears are allowed to soak for 24 h at 4° C, and are then centrifuged. The clear supernatant fluid is then used for testing.

The test is done by drawing about 0·02 ml of the smear extract into a small capillary tube, followed by an equal volume of the antiserum. As this is denser than the extract there is little or no mixing and an interface is clearly visible between the two liquids. Air is then drawn into the tube so that the liquids are near the middle, and the end of the tube is sealed by pushing it into a tray of plasticine. The tubes are left at room temperature for 2 h before being read by an indirect light against a black background. The presence of *Phytodecta* in the meal is shown by the formation of a white precipitate of antigen and antibody combining. This precipitate shows up as a white ring at the junction of the liquids. It is essential that the liquids are perfectly clear for satisfactory results.

A convenient feature of the precipitin test is that both smears and antiserum can be stored and the tests carried out in the winter.

EXPERIMENTAL RESULTS

(*a*) *Meals tested for* Phytodecta

A total of 11 286 gut smears were tested for the presence of *Phytodecta*; 4608

in 1957 and 6678 in 1958. The results from these tests are shown in Table 1. Besides these species, the following were also tested with no positive reaction: 173 *Orthotylus concolor* Kirschbaum (Miridae); 305 phalangids (*Phalangium opilio* L., and *Platybunus triangularis* Herbst); 383 spiders; 19 *Ectobius lapponicus* L. (Dictyoptera); 13 larvae of *Chrysopa* sp.; 29 Coccinellidae; 4 *Cantharis rustica* Fallen, 4 *Rhagonycha limbata* Thomson (Cantharidae); 1 *Nabis flavomarginatus* Scholtz (Nabidae); 6 *Orius niger* Wolff (Anthocoridae). All red mites were tested together, but a sample collected during 1958 was kindly identified by Dr A. M. Massee and Dr E. Collyer. Of 181 specimens only 13 (7·1%) were phytophagous species (*Bryobia sarothamni* Geyskes and *Bryobia* sp.); 164 (90·6%) were the predacious mite *Anystis agilis* Banks and it is almost certainly this species which is feeding on *Phytodecta*. Apart from these the sample contained 1 *Typhlodromus*

Table 1. *Results of precipitin tests*

Figures show the numbers of meals tested and the percentages which reacted with anti-*Phytodecta* and anti-broom sera.

	Anti-*Phytodecta*		Anti-broom	
	Number tested	% reacting	Number tested	% reacting
HETEROPTERA, MIRIDAE				
Heterocordylus tibialis Reuter	1149	3·4	930	5·9
Asciodema obsoletum Fieber	1590	4·2	905	6·4
Orthotylus adenocarpi Perris	2819	4·1	1052	5·7
O. virescens Douglas & Scott	1847	0·9	976	4·3
O. concolor Kirschbaum	173	0	73	6·8
Heterotoma merioptera Scopoli	222	2·2	104	3·8
HETEROPTERA, ANTHOCORIDAE				
Anthocoris nemorum L.	1085	6·3	671	0·7
A. sarothamni Douglas & Scott	187	3·2	119	0
HETEROPTERA, NABIDAE				
Nabis apterus Fabricius	69	1·4	35	0
DERMAPTERA				
Forficula auricularia L.	466	9·2	96	32·2
Red mites	902	1·0	380	0·8

reticulatus, 1 *Nothrus* sp., 1 oribatid larva and 1 larval trombidiid. *Anthocoris nemoralis* Fabricius was found on the broom in very low numbers in 1959 and it is possible that this was overlooked in previous years. If this is so, it would have been included with *A. sarothamni* in the tests. Both species will feed on *Phytodecta* in the laboratory.

Jolivet (1950) records *Anthocoris nemorum* and eight species of Miridae (including *Orthotylus marginalis* Reuter) as predators on *Chrysomela haemorrhoidalis* L., and *Forficula auricularia* as feeding on *Leptinotarsus decemlineata* Say. He also gives fourteen species of Coccinellidae, *Phalangium cornutum* L., several species of spider, and larvae of *Chrysopa* and *Hemerobius* in his list of predators of Chrysomelidae, so that it is possible that positives would have been obtained from some of the other species had larger numbers been tested. Of the predacious mirids and anthocorids only the older nymphs and adults were found to feed upon

the beetle (Table 2). Of a total of 369 first- and 550 second-instar nymphs, no first and only 8 seconds gave a positive *Phytodecta* reaction. Of these, 5 were *Anthocoris nemorum*, 2 *Orthotylus adenocarpi* and 1 *O. virescens*. The influence of the dates of occurrence on the number of *Phytodecta* meals is discussed later (p. 155).

The length of time that a *Phytodecta* meal remains detectable naturally depends on the size of the meal, and on the predator. Individuals of most of the predators were given an egg or larva of *Phytodecta* in the laboratory and the time of feeding noted. Then a known time after feeding (at room temperature) smears were made, so that a series of smears taken from 1 to 48 h after feeding was collected and tested against anti-*Phytodecta* serum. From these tests it was shown that an egg of *Phytodecta* remains detectable in the gut of an earwig for 27-30 h after the meal, while a fourth-instar larva is still detectable 5 days after being eaten. On the other hand an *Anthocoris nemorum* (IV-Adult) gives a positive reaction for *Phytodecta* for 17-20 h after eating an egg, or 24-28 h after eating a first-instar larva. Similarly *Phytodecta* can be shown present in the gut of *Heterocordylus* (II, III, IV, Adult)

Table 2. *The percentage of meals from mirid and anthocorid predators reacting with anti-*Phytodecta *serum*

The figures in parentheses show the number tested.

	Predator instars					
	I	II	III	IV	V	Adult
Heterocordylus	–	–	0 (20)	1·0 (191)	3·4 (467)	4·5 (473)
Asciodema	0 (18)	0 (106)	5·6 (249)	6·6 (330)	4·1 (340)	2·5 (641)
Orthotylus adenocarpi	0 (97)	1·2 (173)	5·9 (406)	7·6 (435)	4·6 (504)	2·5 (1361)
O. virescens	0 (148)	0·9 (110)	0 (151)	1·2 (244)	2·2 (228)	0·8 (842)
Heterotoma	0 (20)	0 (16)	5·9 (17)	7·1 (14)	0 (18)	1·6 (72)
Anthocoris nemorum	0 (79)	3·8 (130)	3·4 (203)	9·3 (203)	6·0 (200)	9·6 (272)
A. sarothamni	0 (7)	0 (15)	3·6 (28)	0 (30)	3·7 (27)	4·2 (72)

and *Orthotylus adenocarpi* (V) for 18-22 h after feeding on an egg, or 24-26 h after eating a first-instar larva. *Nabis apterus* (adult) still reacts up to 48 h after feeding on a fourth-stage larva.

During the course of this work it was found that mirid and anthocorid predators would not feed on anything bigger than a second-stage larva of *Phytodecta*. *Forficula* and *Nabis* would, however, readily accept fully grown fourth-stage larvae. It was therefore assumed that a positive reaction from a smear of a mirid or anthocorid showed that it had fed on the beetle within the past 24 h. Similarly, a positive from an earwig smear was taken as showing that it had fed in the past 60 h.

(*b*) *Meals tested for broom*

Over the 2 years 5952 smears were tested against anti-broom serum. The results of these tests are shown in Table 1, where it will be seen that the mirids were all feeding to about the same extent, about 5% of the populations reacting to the serum. A small number of *Anthocoris nemorum* (0·7%) showed a positive reaction,

indicating that this species does take some plant food. No positives were obtained from *A. sarothamni*. Only 119 individuals were tested, however, so that this species could have been feeding on broom to the same extent as *A. nemorum* without necessarily giving a positive. An adult of *A. sarothamni* was seen feeding on broom in the laboratory and its smear reacted with antibroom serum, so that this species also probably takes some plant food. *Nabis apterus* gave no positives for broom and I think it extremely unlikely that it takes plant food; only 35 individuals were, however, tested. Of 380 red mites tested, only 3 (0·8%) had fed on broom. As was described earlier, all the mites were lumped together in these tests, and the proportion of phytophagous species in the samples was very small.

The serum used in these tests was not as sensitive as that used in testing for *Phytodecta*. The main reason for this was that the neutralization of its reaction with gorse was difficult and left it greatly reduced in sensitivity. Smears taken a known time after feeding showed that a broom feed remains detectable in an earwig for about 36 h, while *Heterocordylus* (I-IV) reacts for only 8-10 h after feeding.

The possibility that a predator might give a reaction for broom after feeding on a phytophagous prey, was considered. However, predators that had fed upon *Phytodecta* larvae and aphids gave no reaction for broom. The chances of a predator taking in this way sufficient broom material to be detected would, of course, be small, particularly as most of the predators of *Phytodecta* are Heteroptera and only suck the body juices of their prey.

THE PREDATORS OF *PHYTODECTA*

(*a*) *Life cycles*

The dates of hatching of the various predators of *Phytodecta* are different, so that their life cycles do not all overlap with the beetle to the same extent, and there is a succession of predators occurring through the *Phytodecta* season (Fig. 1). All of the Miridae overwinter in the egg stage and hatch in spring (Waloff & Southwood 1960). The first to start hatching is *Heterocordylus* in late March or early April, and adults start emerging by the end of May or the beginning of June. All have died by mid-July so that this species is present only at the beginning of the beetle's season. *Asciodema* and *Orthotylus adenocarpi* are the next two species to hatch, *Asciodema* being the earlier by about a week. Both species hatch in late April or early May, so that their older nymphs coincide fairly well with the peak in *Phytodecta* numbers. Both species have died by the end of August. At the end of May, *Orthotylus virescens* hatches together with *Heterotoma merioptera*. The larger nymphs of both these species miss the peak of *Phytodecta*, although young stages of the beetle are still numerous. *Orthotylus concolor* is the last of the mirids to hatch (mid- to late June) and its older nymphs miss the greater part of the beetle's season. None of this species was shown to have fed on *Phytodecta*.

The two species of *Anthocoris* overwinter as adults and lay their eggs in early spring. These hatch at the end of April and produce adults by mid-June. In both 1957 and 1958, a second generation of both species of *Anthocoris* was produced,

hatching in mid-July and becoming adult by the beginning of September. Hill (1957) has shown that *A. nemorum* is univoltine in Scotland, while it has two generations in southern England (Collyer 1953 and Sands 1957), and appears to have three generations in France (Bonnemaison & Missonier 1956). It is likely that the same applies to *A. sarothamni*, and that the number of generations that both these species can fit into a year is dependent upon summer temperatures. Predacious stages of both species of *Anthocoris* are present throughout the *Phytodecta* season. *Nabis apterus* hatches in early April and becomes adult by mid-July. It is therefore present right through the beetle season. *Forficula* is in very low numbers

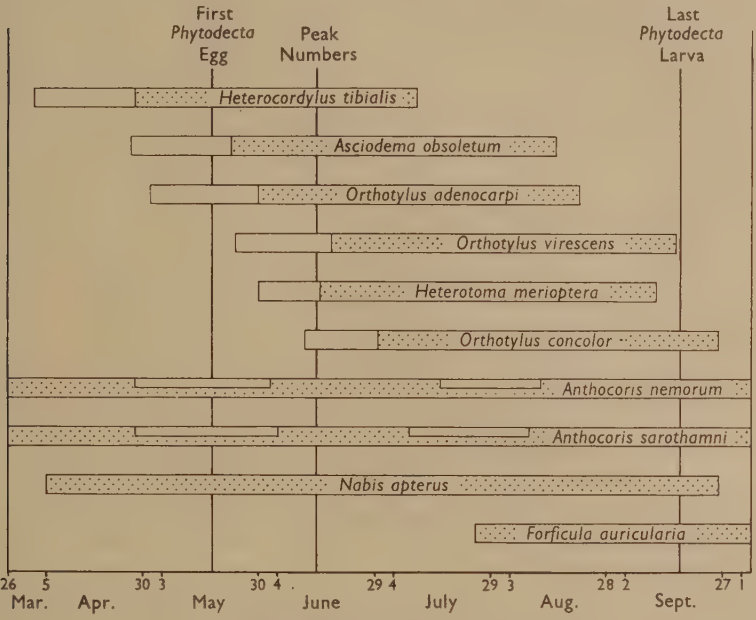


Fig. 1. The time of occurrence of various predators compared with that of *Phytodecta*. The stippled areas indicate predaceous stages.

on the broom during the early part of the year, but becomes numerous from late July onwards, when they are particularly common in dehisced seed pods.

It will be seen from this that the number of *Phytodecta* prey available is very different for each species. This accounts for the differences seen in Table 2. The beetle's eggs and larvae are present only during the later instars of *Heterocordylus*, and as might be expected, the larger and more active adult stage is the most predacious. *Heterotoma* and *Orthotylus virescens* have plenty of the beetle young stages present during their early instars, but it is not until the third or fourth instar that the nymphs are large enough to prey on the beetle. Again, it is the larger nymphs and adults of *Asciodema* and *Orthotylus adenocarpi* that are feeding on *Phytodecta*. Here, however, it is the third and fourth instars that give the

highest percentage of positive meals. This is due to the much higher number of *Phytodecta* present at that time. Both species of *Anthocoris* show a higher rate of predation during the larger and more active stages.

(*b*) *Alternative food*

As was seen earlier, many of the predators of *Phytodecta* are omnivorous. Also, even the truly carnivorous species are not specific in their choice of food and attack many prey besides *Phytodecta*. *Anthocoris nemorum* is the most widely distributed of the predators and it is found on very many plants besides broom. It appears to be mainly carnivorous, and will feed on almost any small arthropod. A list of all its recorded prey is given by Hill (1957). At Silwood Park, alternative prey to *Phytodecta* are numerous. It has been seen feeding on the two broom aphids, *Aphis sarothamni* Franssen and *Acyrthosiphon spartii* Koch, nymphs and adults of *Arytaina genistae* Latreille (Psyllidae), small caterpillars and spiders, and it undoubtedly will take Collembola, Psocoptera and Miridae. *Anthocoris sarothamni* probably feeds on a similar range of prey, and will readily take the two broom aphids in the laboratory. Unlike *A. nemorum* it is confined to broom.

The three species of *Orthotylus* are confined to broom. Nothing is yet known about the food of *O. concolor*, as it occurs in extremely low numbers, but both *O. adenocarpi* and *O. virescens* are omnivorous and will take aphids in the laboratory. *O. adenocarpi* is more predacious on the eggs of *Phytodecta* than *Orthotylus virescens*. Over the course of a week in the laboratory, twelve adults of *O. adenocarpi* consumed *Phytodecta* eggs at an average rate of one every 13·9 h; twelve adults of *Orthotylus virescens* only took eggs at a rate of one every 44·4 h over the same week (*cf.* Table 4). Large nymphs of *O. adenocarpi* will feed upon the young stages of other Miridae in the laboratory.

Asciodema obsoletum occurs on gorse and broom (Butler 1923). Its feeding habits are very similar to *Orthotylus adenocarpi* and it will readily take aphids. The same applies to *Heterocordylus tibialis*. Butler gives this species as inhabiting broom and *Genista*. *Heterocordylus* will feed on the young stages of other Miridae in the laboratory. *Heterotoma merioptera* is a widespread mirid, recorded from many plants (Butler 1923, Kullenberg 1946). It is omnivorous and is recorded by Kullenberg as feeding on Lepidopterous eggs and larvae and on aphids. *Nabis apterus* occurs on many trees and shrubs and is probably entirely predacious. It will take a variety of prey, but feeds particularly readily on mirids and psyllids in the laboratory. These probably make up much of its food on broom. The earwig, *Forficula auricularia* is omnivorous and a scavenger. It will eat a wide range of things, alive or dead.

Most of the alternative prey recorded here are far more numerous than *Phytodecta* and it seems likely that the beetle forms a very small part of the diet of all these predators.

(*c*) *The likelihood of multiple feeds*

From the precipitin test we obtain an estimate of the proportion of the predator

population that has fed on the beetle within a certain number of hours. There is, however, no way of knowing whether more than one *Phytodecta* was taken in that time.

Now the eggs of *Phytodecta* are not laid in groups but are scattered over the broom plants. The young larvae tend to be on the younger leaves, but occur in sufficiently low numbers to be fairly evenly scattered. This means that some idea of the likelihood of a predator finding more than one can be obtained from the mobility of the predator and the mean distance between the beetles' eggs and larvae. A rough estimate of the rate of movement of many of the predators was obtained by watching individuals in the field (Table 3). During the period when *Phytodecta* eggs and young larvae were most abundant a mean rate of movement of 1·14 cm/min was required in 1957 for more than one to be found in a day; in

Table 3. *The average rate of movement of some of the predators in the field*

The figures in parentheses are the numbers of individuals included in the observations.

		Time observed (min)	Rate of movement (cm/min)	Average screen temperature (° F)
Asciodema	IV	385 (6)	0·10	60·0
	V	180 (3)	0·17	73·2
Orthotylus adenocarpi	IV	375 (5)	0·27	60·7
	V	695 (7)	0·31	68·4
	Ad	530 (5)	0·40	73·5
O. virescens	IV	120 (2)	0·15	76·2
	V	225 (3)	0·09	68·0
	Ad	530 (4)	0·12	71·3
Heterotoma	Ad	65 (1)	3·35	64·8
Heterocordylus	V	205 (4)	1·09	63·3
	Ad	265 (10)	0·80	62·6
Anthocoris nemorum	III	120 (1)	2·18	65·3
	V	150 (5)	2·36	66·2
	Ad	85 (2)	6·68	66·7

1958 a rate of 1·29 cm/min was required. These figures are based on estimates by Richards and Waloff of *Phytodecta* numbers and the total length of broom in the area.

The mirids in particular move very little, especially in cloudy or windy weather. Of those predators considered, only *Heterotoma*, *Anthocoris nemorum* and possibly *Heterocordylus* move sufficiently fast to be able to find more than one, when the prey numbers were highest. When it is remembered that alternative prey (particularly aphids and psyllids) were far more numerous than the beetle even at this time, it is very unlikely that multiple *Phytodecta* meals are being regularly taken. In 1957, during the peak period in beetle numbers, aphids and psyllids combined outnumbered them by at least seven to one. In the same period in 1958 they outnumbered the beetle by nine to one. Unfortunately these observations had to be made at odd times when other work permitted. However, some experiments

in the laboratory do indicate that multiple feeds are likely to be extremely rare.

Twelve adults of *Orthotylus adenocarpi*, *O. virescens*, *Heterotoma* and *Anthocoris nemorum* were confined each in a 3 × 1 in. tube. Three *Phytodecta* eggs were placed in each tube and any eaten eggs replaced every 4 h. The number taken during 1 week are shown in Table 4. Some individuals died during the experiment so that the accumulated time is not the same for each species.

Table 4. *Rates of predation by some predators of* Phytodecta *in the laboratory*

	Time (h)	Number eaten	Average rate of predation
Orthotylus adenocarpi	776	56	1 egg every 13·9 h
O. virescens	888	20	1 egg every 44·4 h
Heterotoma	1026	90	1 egg every 11·4 h
Anthocoris nemorum	1364	107	1 egg every 12·8 h
	1202	93	1 larva every 12·9 h

With a plentiful supply of *Phytodecta* none of these predators averaged more than one prey every 11 h, so it is probably safe to assume that more than one *Phytodecta* is not regularly taken in the time that a meal would remain detectable. It will be shown later that calculations based on this assumption give very reasonable estimates of the number of *Phytodecta* taken by each species of predator.

(*d*) *The size of the predator populations*

Throughout the summer the numbers of the various predators were estimated once or twice a week. This was done by shaking fifty standard armfuls of broom on to a white beating tray in the same way as Richards and Waloff sample the adult *Phytodecta* population. This method is satisfactory for large insects, but many of the young stages (first and second instars) of the mirids and anthocorids were undoubtedly missed and their numbers underestimated. This was particularly so in 1957, but since the very young stages of these bugs do not feed on the beetle, this error is not important. The total number of armfuls of broom in the area was estimated by Professor Richards and Dr Waloff at the beginning and end of the season, and their figures were used here to calculate the total number of each predator present. The estimated numbers of each predator during the time when the beetles eggs and larvae were available in each year is shown in Fig. 2. It will be seen that the general picture obtained is very similar for the 2 years. The total number of predators was somewhat higher in 1958 when a peak of 52 000 was reached on 11 June, as compared with a peak of 44 000 on 6 June 1957. This increase was almost entirely due to an increased number of *Orthotylus adenocarpi* in 1958, when a peak of 23 000 was reached, as compared with 16 000 in the previous year. The numbers of *Heterocordylus*, *Asciodema* and *Orthotylus virescens* were very similar in the 2 years, while *Nabis* and *Heterotoma* were slightly more numerous in 1958 than in 1957, though in both years their numbers were extremely low. The numbers of both species of *Anthocoris* varied in a similar way, though

A. nemorum was always by far the more numerous. The spring generation of both species was small in 1957, but gave rise to a large second generation. Mortality during the winter must have been low, as the spring generation was quite large in 1958. However, both species had a very small second generation that year.

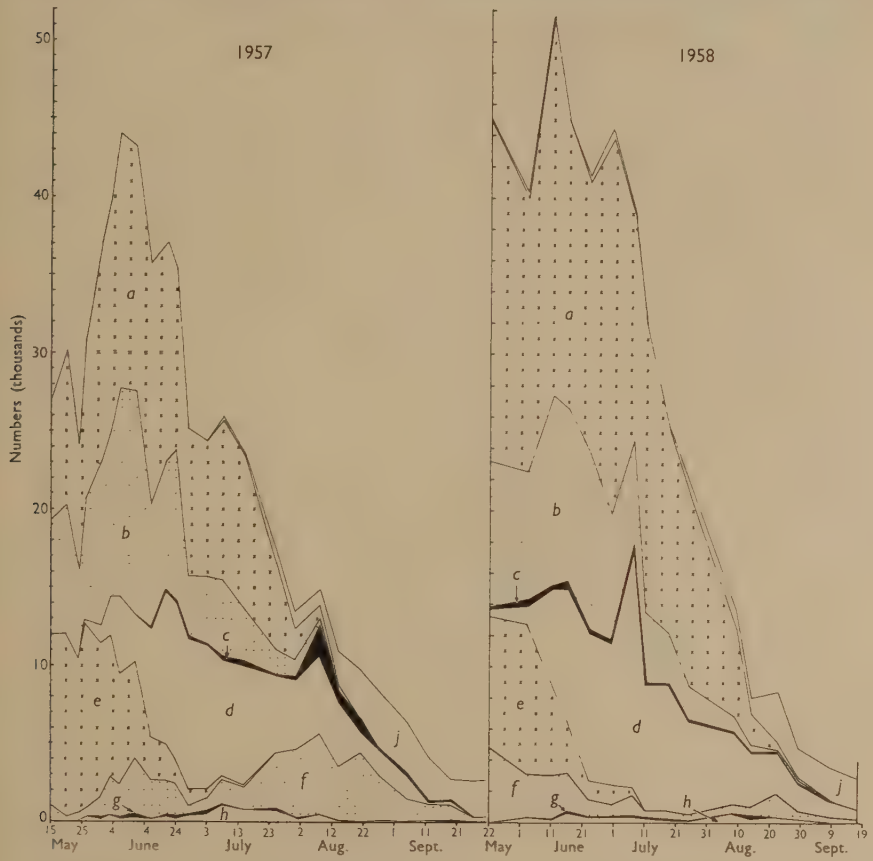


Fig. 2. Predator numbers in 1957 and 1958:
a, Orthotylus adenocarpi
b, Asciodema obsoletum
c, Anthocoris sarothamni
d, Orthotylus virescens
e, Heterocordylus tibialis
f, Anthocoris nemorum
g, Nabis apterus
h, Heterotoma merioptera
j, Forficula auricularia

(*e*) *The number of* Phytodecta *taken*

Now, if it is assumed that one beetle is destroyed for each meal that contains *Phytodecta* (the likelihood of this being correct is discussed on p. 157), an estimate of the number of *Phytodecta* taken by each predator may be obtained. This is calculated from the proportion of meals containing *Phytodecta* and the estimated

number of the predator present, bearing in mind the length of time that a meal will remain detectable. For example, on 18 June 1958 a sample of 200 *Orthotylus adenocarpi* contained six meals which reacted with anti-*Phytodecta* serum. Now we know that a beetle meal will remain in the gut of *Orthotylus* for approximately 24 h, and it is estimated that 12 625 *O. adenocarpi* were present on 18 June, so that the number of beetles consumed by that predator during the previous 24 h

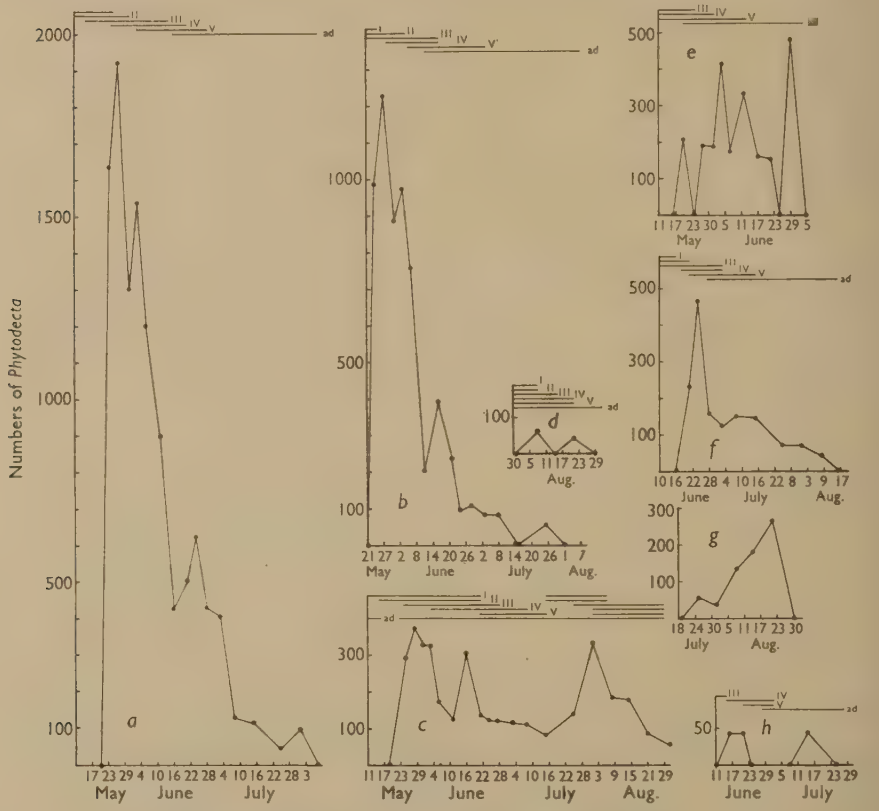


Fig. 3. The estimated numbers of *Phytodecta* taken by various predators in 1957:
a, Orthotylus adenocarpi
b, Asciodema obsoletum
c, Anthocoris nemorum
d, A. sarothamni
e, Heterocordylus tibialis
f, Orthotylus virescens
g, Forficula auricularia
h, Heterotoma merioptera

was $6 \times 12\,625 \div 200 = 379$. Estimates of the number of beetles taken by each predator were calculated in this way for each sampling day and the results are shown in Figs. 3 and 4.

O. adenocarpi ate most *Phytodecta* in both years; the number taken rose rapidly to a peak on 27 May 1957 and 11 June 1958 and then fell. The maximum number of the prey was reached on 18 June 1957 and 11 June 1958. *Asciodema* showed a

similar pattern, though the peak attained was lower in both years. *Orthotylus virescens* had a marked peak in predation in 1957 at a time when fourth- and fifth-instar nymphs were present; these missed the highest *Phytodecta* numbers. In 1958 the number taken was smaller and there was no clear pattern of predation. *Anthocoris nemorum* showed two distinct peaks of predation in 1957. The first coincided with its first generation and a high population of the prey; the second peak was almost as high as the first although the number of prey present at that time was lower. This was because of the comparatively large number of *Anthocoris* in the second generation. In 1958 the second generation occurred later and was small, and there was no distinct second peak in the number of beetles taken. *Forficula* ate most beetles at the very end of the season when they (*Forficula*) became numerous on the broom. All other species fed at a very low rate on *Phytodecta*.

Estimates of the total number taken by each predator are given by the areas under the curves shown in Figs. 3 and 4; these estimates are shown in Table 5. Some idea of the reliability of these figures is given by the population estimates

Table 5. *Estimated numbers of* Phytodecta *taken by each predator in* 1957 *and* 1958

	1957	1958
Heterocordylus tibialis	8935	9000
Asciodema obsoletum	23 825	29 277
Orthotylus adenocarpi	44 780	48 365
O. virescens	7332	3482
Heterotoma merioptera	892	375
Anthocoris nemorum	17 660	7500
A. sarothamni	689	864
Nabis apterus	43	0
Forficula auricularia	4692	1675
Red mites (*Anystis agilis*)	2733 (?)	724 (?)
Totals	111 581	101 262

obtained by Richards and Waloff (in preparation). They calculate that 201 760 eggs were laid by *Phytodecta* in 1957, of which 156 934 died before pupation. Of these 11 593 can be accounted for by infertility, parasitism, etc., which leaves 145 341 which must have been killed by predators or some other factor. The estimate of 111 581 obtained from these tests does then appear to be reasonable. For 1958 Richards and Waloff estimate that 125 039 eggs were laid and that 117 443 of these died during egg and larval development. Known factors leave 107 284 unaccounted for, so that again the figure of 101 262 for the effect of predation is of the right order. The agreement between the figures obtained from these tests and the completely independent estimates of Richards and Waloff suggest that the important predators were all identified by the technique, and that these predators accounted for the greater part of beetles' disappearance during the egg and larval stages in both 1957 and 1958. Some of the eggs and larvae accounted for by parasitism and infertility would of course have been eaten by the predators in both years (Richards & Waloff, loc. cit.). The figures obtained by Richards & Waloff confirm the pattern of predation seen from these tests. In both years

they found that the greatest drop in *Phytodecta* numbers occurred during the egg and first larval instar (99·5% of the drop in 1957, and 94·3% in 1958). Laboratory experiments have shown that only *Nabis* and *Forficula* would feed on *Phytodecta* larvae after they had reached the second instar. In other words all those taken by mirids, anthocorids and mites would have been very young stages. These represent 95·8% of the total taken in 1957 and 98·2% in 1958.

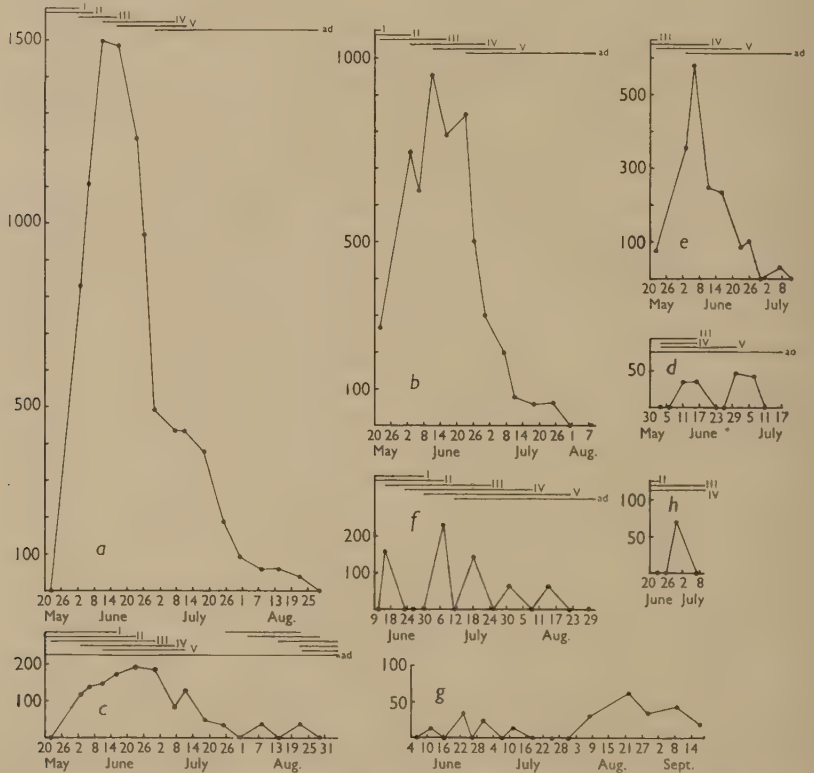


Fig. 4. The estimated numbers of *Phytodecta* taken by various predators in 1958. For key see Fig. 3.

DISCUSSION

Although *Phytodecta* has only one generation a year, it has a long period of oviposition and its young stages are present from the middle of May until the end of September. The greatest number of eggs are, however, laid in spring, so that there is a distinct peak in the number of eggs and larvae in the middle of June. Throughout the summer predators are numerous, but at different times different species are most important. Thus the mirids hatch in succession through the spring and early summer, so that the first species to hatch (*Heterocordylus tibialis*), has died out by mid-July, while the last (*Orthotylus virescens*), survives until the

Table 6. *Rates of feeding by the various predators upon* Phytodecta

Predator	Dates during which prey and predator occurred	Average daily number predator present (III-Ad)	Average daily number *Phytodecta* present (Egg-II)	Average number predator per prey	Number *Phytodecta* taken per day	% available *Phytodecta* taken by each individual predator per day ($\times 10^{-4}$)
	1957					
Heterocordylus	15 May-8 July	4820	29 850	0·16	162·5	1·12
Asciodema	15 May-8 Aug.	5520	29 760	0·18	277·0	1·69
Orthotylus adenocarpi	15 May-14 Aug.	9500	28 860	0·33	486·7	1·78
O. virescens	11 June-12 Sept.	4970	23 200	0·21	78·0	0·68
O. concolor	24 June-26 Sept.	730	17 260	0·04	0	0
Heterotoma	11 June-9 Sept.	350	21 650	0·02	9·8	1·43
Anthocoris nemorum	15 May-3 Oct.	1510	19 750	0·08	124·4	4·17
A. sarothamni	15 May-3 Oct.	220	19 750	0·01	4·9	0·91
Nabis apterus	15 May-26 Sept.	140*	23 910†	0·006	0·3	0·07
Forficula	25 July-3 Oct.	2160*	13 270†	0·16	66·1	2·31
	1958					
Heterocordylus	22 May-11 July	5160	21 930	0·23	176·5	1·55
Asciodema	22 May-14 Aug.	5700	19 430	0·29	344·4	3·11
Orthotylus adenocarpi	3 June-29 Aug.	10 860	19 090	0·57	549·6	2·65
O. virescens	16 June-17 Sept.	4840	13 320	0·36	37·0	0·58
O. concolor	7 July-17 Sept.	430	11 920	0·04	0	0
Heterotoma	16 June-8 Sept.	180	14 300	0·01	4·4	1·67
Anthocoris nemorum	22 May-17 Sept.	850	16 060	0·05	63·0	4·59
A. sarothamni	22 May-17 Sept.	190	16 060	0·01	7·3	2·11
Nabis apterus	3 June-17 Sept.	80*	18 670†	0·004	0	0
Forficula	25 July-17 Sept.	1610*	13 720†	0·12	30·5	1·37

* All stages. † Egg-IV.

middle of September. The two species of *Anthocoris* are present throughout the summer, but are most numerous at the times that the two generations hatch. *Nabis apterus* is present in low numbers throughout, while *Forficula* is important only at the very end of the season. As the various species of predator do not all occur at the same time, the number of *Phytodecta* available to each is not the same. Table 6 shows the average daily numbers of beetles available and the rate of feeding of each predator. From this it will be seen that in both years *Anthocoris nemorum* was by far the most predacious. This species is primarily carnivorous while many of the others (*e.g.* the mirids and *Forficula*) are more omnivorous. It does, however, show a greater liking for *Phytodecta* than either *Anthocoris sarothamni* or *Nabis apterus*, both of which are also carnivorous. One would suspect that *Anthocoris sarothamni* is more specific in its choice of prey, since it is confined to broom, while *A. nemorum* is extremely widespread. Obviously its main source of food is not *Phytodecta*. The same applies to *Nabis* and this attacks mirids and psyllids so readily in the laboratory, that these probably are preyed upon heavily in the field.

The mirids also do not all feed on the beetle to the same extent. All are omnivorous and will also take prey other than *Phytodecta*. The number of *Phytodecta* prey available is largely dependent on the time of occurrence of the predator. Thus *Heterocordylus* must depend little upon the beetle since this is not present for much of its life cycle. The rate of feeding is not, however, totally dependent upon the availability of the prey. Laboratory experiments show that *Orthotylus adenocarpi* takes the beetle far more readily than does *O. virescens*. *O. concolor* obviously feeds even less on *Phytodecta*, since if it were feeding even as much as *O. virescens*, at least one positive would have been expected from the 173 smears tested. Obviously the feeding habits of these mirids differ between species.

The distribution of the beetles' numbers was rather different in the 2 years (Richards & Waloff, in preparation). About half as many eggs again were laid in 1957 as in the following year. The peak number was, however, about the same in both years, but laying continued at a high rate longer into the summer in 1957.

There is another factor to be considered when comparing the number of *Phytodecta* taken in the 2 years. Broom is a comparatively short-lived plant and rarely survives more than 12-15 years. Richards and Waloff (in preparation) have shown that recent winters have killed many of the bushes in this area. In 1957 they estimated that there were 2160 armfuls of broom in the area, but the winter of 1957-58 killed about a third, so that there were only 1400 armfuls in the following year. These factors make it rather difficult to compare the rates of predation in the 2 years. An attempt to do so is shown in Table 7, in which the number of predators and prey per armful of broom is given for the 2 years, together with the percentage of available prey that were taken. Unfortunately, there is very little difference in the density of either the prey or the predators in the 2 years. What differences there are do, however, show, as one would expect, that a greater percentage of beetles is taken when the density of predators is highest. This is best seen in *Asciodema* and *Orthotylus adenocarpi* which were both present at a

higher density in 1958 and consumed a higher proportion of the *Phytodecta* population, although this was almost identical in size to that in the previous year. It is unlikely that a clear picture of the influence of the number of prey on the percentage eaten would have emerged, even if the 2 years had not been so similar. None of these predators is specific in its attack on the beetle and the latter is greatly outnumbered by alternative prey. Probably aphids and psyllids are the most numberous alternative prey to the mirids and anthocorids. It is likely, moreover, that with the succession of mirids through the summer the older stages of the early species feed upon the young stages of others. *Heterocordylus* will readily feed on young stages of *Orthotylus adenocarpi* and older nymphs of *O. adenocarpi* will feed on young stages of *O. virescens* in the laboratory. The mirids are also probably regularly taken by *Nabis* and the anthocorids. Obviously the

Table 7. *The prey and predator densities and rates of predation in* 1957 *and* 1958

		Average number of predator per armful	Average number of *Phytodecta* per armful	% available *Phytodecta* taken per day
Heterocordylus tibialis	1957	2·23	13·82	0·54
	1958	3·68	15·66	0·80
Asciodema obsoletum	1957	2·56	13·78	0·93
	1958	4·07	13·88	1·77
Orthotylus adenocarpi	1957	4·40	13·36	1·69
	1958	7·75	13·63	2·88
O. virescens	1957	2·30	10·74	0·34
	1958	3·46	9·25	0·28
Heterotoma merioptera	1957	0·16	10·02	0·05
	1958	0·13	10·21	0·03
Anthocoris nemorum	1957	0·70	9·14	0·63
	1958	0·61	11·47	0·39
A. sarothamni	1957	0·10	9·14	0·02
	1958	0·14	11·47	0·04
Nabis apterus	1957	0·06	11·07	0·001
	1958	0·06	13·34	0
Forficula auricularia	1957	1·00	6·15	0·50
	1958	1·15	9·80	0·22

picture is an extremely complicated one, and without a detailed study of the type and quantity of alternative food taken by these predators, little can be said as to the factors governing the number of beetles taken.

The figures on p. 161 show that very reasonable estimates of the numbers of *Phytodecta* destroyed by each predator were obtained from the precipitin test. This test has, however, certain limitations which may prevent it being as useful in other predator-prey investigations. The precipitin test is highly sensitive, but not completely specific in its reaction. The anti-*Phytodecta* serum used here reacted with other Chrysomelidae, Cassididae and Coccinellidae. Fortunately it was found possible to remove the reaction to Coccinellidae by absorption, and Chrysomelidae other than *Phytodecta*, and Cassididae were rare on the broom. In other studies this reaction with other closely related insects might be a more

serious problem. Other workers have encountered this problem. Hall, Downe, MacLellan & West (1953) found that serum obtained against the forest tent caterpillar (*Malacosoma disstria*) reacted with the eastern tent caterpillar (*M. americanum*); also anti-mosquito serum reacted strongly with Chironomidae and Chaoboridae, while serum obtained against the codling moth (Tortricidae) reacted with a number of species of this and the closely related family Olethreutidae. Similarly, Fox & MacLellan (1956) studying the predators of a wireworm (*Agriotes sputator*) found that their anti-serum reacted with all other Elateridae that they tested, including *Athous affinis* which probably preyed on *Agriotes*. Refinement of the anti-serum by absorption results in the loss of some of its sensitivity. This may not be important if the unwanted reaction is with a fairly remote species as in the case of the anti-*Phytodecta* serum with Coccinellidae. If the unwanted reaction is with a closely related species, however, absorption may reduce the sensitivity of the serum to such an extent as to make it useless.

A positive from this test only tells one that the predator has fed upon the prey, it does not show how many prey were consumed. To make the test quantitative an assumption has to be made of the likely number of prey making up a meal. In an insect such as *Phytodecta* which is not numerous and is scattered over the host plant, multiple feeds are probably rare (p. 157). Where a numerous prey or one which lives in colonies (*e.g.* Aphidae) is concerned, it will be extremely difficult to get a reasonable estimate of the number of prey taken.

ACKNOWLEDGMENTS

Before starting this work I spent a month at the Lister Institute of Preventive Medicine, Elstree, learning something of serological techniques, and I should like to thank Mr B. Weitz and his staff for their kind help and encouragement during this time. I am also indebted to Professor O. W. Richards and Dr N. Waloff, not only for the liberal use of their data, but also for introducing me to the problem. I should also like to thank Miss T. Dedman who helped with the tedious routine of sampling and testing. This work was financed by a grant from the Agricultural Research Council.

SUMMARY

1. Predators of the broom beetle *Phytodecta olivacea* were studied using the precipitin test. This identifies *Phytodecta* in the gut of a recently fed predator by its reaction with antibodies in the blood serum of rabbits which have been inoculated with an extract of the beetle.

2. The gut contents of 11 286 predators were tested, and five species of Miridae, two Anthocoridae, one nabid, an earwig and a red mite were shown to regularly feed on the beetle. Of the Miridae and Anthocoridae, only the older nymphs and adults preyed on *Phytodecta*.

3. All these predators readily fed on beetles' eggs and young larvae in the laboratory but only *Nabis* and *Forficula* would take larvae older than the second instar.

4. A *Phytodecta* meal remains detectable for about 24 h after being eaten by a mirid or an anthocorid, while *Forficula* still reacts 30 h after eating an egg and 5 days after eating a fully grown larva.

5. The number of beetles taken by each predator was largely dependent upon the time of occurrence of it compared with the prey. Thus the mirids hatch in succession through the spring and the number of *Phytodecta* available to each is different.

6. The number of predators was estimated by regular sampling of the broom, while the prey population was also regularly sampled by Professor Richards and Dr Waloff.

7. It was estimated that predators accounted for 111 600 beetles in 1957 and 101 300 in 1958. These figures agree very closely with estimates made by Richards & Waloff of the disappearance of eggs and larvae in the 2 years.

8. None of the predators is specific in its attack, and alternative prey greatly outnumber the beetle. Only a very low proportion of the population of each predator was shown to have fed on *Phytodecta* at any one time, and it seems certain that the beetle forms a very small part of the diet of all the species.

REFERENCES

Bonnemaison, L. & Missonier, J. (1956). Le Psylle du Poirier (*Psylla pyri* L.). Morphologie et Biologie; méthodes de Lutte. *Ann. Epiphyt.* **2,** 263-331.

Brook, M. M. & Proske, H. O. (1946). Precipitin test for determining natural insect predators of immature mosquitoes. *J. Nat. Malaria Soc.* **5,** 45-56.

Butler, E. A. (1923). *A biology of the British Hemiptera-Heteroptera.* London.

Collyer, E. (1953). Biology of some predatory insects and mites associated with the fruit tree red spider mite (*Metatetranychus ulmi* (Koch)) in south-eastern England. II. Some important predators of the mite. *J. Hort. Sci.* **28,** 85-97.

Dempster, J. P., Richards, O. W., & Waloff, N. (1959). Carabidae as predators on the pupal stage of the chrysomelid beetle, *Phytodecta olivacea* (Forster). *Oikos,* **10,** 65-70.

Fox, C. J. S. & MacLellan, C. R. (1956). Some Carabidae and Staphylinidae shown to feed on a wireworm, *Agriotes sputator* (L), by the precipitin test. *Canad. Ent.* **88,** 228-31.

Hall, R. R., Downe, A. E. R., MacLellan, C. R. & West, A. S. (1953). Evaluation of insect predator-prey relationships by precipitin test studies. *Mosquito News,* **13,** 199-204.

Hill, A. R. (1957). The biology of *Anthocoris nemorum* (L) in Scotland (Hemiptera: Anthocoridae). *Trans. R. Ent. Soc. Lond.* **109,** 379-94.

Jolivet, P. (1950). Les parasites, prédateurs et phorétiques des Chrysomeloidea (Coleoptera) de la faune franco-belge. *Bull. Inst. Sci. nat. Belg.* **26,** No. 34.

Kullenberg, B. (1946). *Studien über die Biologie der Capsiden.* Uppsala.

Leone, C. A. (1947). A serological study of some Orthoptera. *Ann. Ent. Soc. Amer.* **40,** 417-33.

McFarlane, A. S. (1942). Behaviour of lipoids in human serum. *Nature, Lond.* **149,** 439.

Proom, H. (1943). The preparation of precipitating sera for the identification of animal species. *J. Path. Bact.* **55,** 419-26.

Sands, W. A. (1957). The immature stages of some British Anthocoridae (Hemiptera). *Trans. R. Ent. Soc. Lond.* **109,** 295-310.

Waloff, N. & Richards, O. W. (1958). The biology of the chrysomelid beetle *Phytodecta olivacea* (Forster) (Coleoptera: Chrysomelidae). *Trans. R. Ent. Soc. Lond.* **110,** 99-116.

Waloff, N. & Southwood, T. R. E. (1960). The immature stages of mirids (Heteroptera) occurring on broom (*Sarothamnus scoparius* (L.) Wimmer) with some remarks on their biology. *Proc. R. Ent. Soc. Lond.* (A) **35,** 39-46.

Weitz, B. (1952). The antigenicity of sera of man and animals in relation to the preparation of specific precipitating antisera. *J. Hyg. Camb.* **50,** 275-94.

THE BEHAVIOUR OF THE STALKED INTERTIDAL BARNACLE *POLLICIPES POLYMERUS* J. B. SOWERBY, WITH SPECIAL REFERENCE TO ITS ECOLOGY AND DISTRIBUTION

By H. BARNES*

The Marine Station, Millport

and E. S. REESE

Department of Zoology, University of California, Los Angeles

(With Plates 4-7 and 6 Figures in the Text)

The stalked cirripede, *Pollicipes polymerus*, is one of the commonest animals in the mid-tide region of the more exposed parts of the North American Pacific coast (Ricketts & Calvin 1952). Solitary individuals are rare and, even when present, close examination suggests that they are often the remnant of an extensive population. Solitary individuals have been found in situations where there is considerable abrasion by sand scouring and it is then often possible to trace the gradual degeneration of massive clumps through to isolated animals. Furthermore, in such places *Mytilus* is similarly affected. Characteristically, the species occurs in dense aggregates usually mixed with *Mytilus californianus* to form the distinctive *Pollicipes* (*Mitella*)-*Mytilus* community, which covers extensive areas of rocks, boulders and artificial structures (Pl. 5, *A* and *B*); this association provides shelter for numerous other animals, in particular crustaceans, flat worms, and annelids. The species is usually absent from both sheltered bays and estuaries. The form of the aggregate or clump depends largely upon both the degree of exposure to wave action and the micro-environment. In exposed situations they are dense, with individual peduncles strong, relatively short, and attached over a considerable basal area; in less exposed places where there is much sand the clumps, although still firm and solid, contain much sand as well as entangled debris. In such quieter situations as well as amongst the more sheltered mussel beds, the peduncles are often greatly elongated, have relatively few calcareous scales and taper towards the base (Pl. 4*B*), so that each has only a relatively small area of attachment; these elongated peduncles ramify through the clump and ultimately bring their capitula into a position where, in spite of the constant accumulation of debris, feeding may be effectively carried out (Pl. 4*C*). It may be noted that the development of the deep purple colour of the peduncle seems to be in part dependent upon exposure to light; the more distal parts of the attenuated peduncles in a debris-packed clump are light orange in colour. When the surrounding debris and other animals are taken away so that the base of such a light coloured peduncle is exposed, it turns

* I wish to acknowledge leave of absence granted by the Council of the Scottish Marine Biological Association and support from the National Science Foundation (Grant G. 3235 to Professor T. H. Bullock) and the Office of Naval Research (Contract No. NR. 165/142 to Dr D. L. Ray).

deep purple within a few days; whether the pigment is formed under the influence of light or whether only migration to the epidermis of pre-formed pigment or its precursor (the peduncular fluid is strongly pigmented) is involved, is not known.

With few exceptions (see pp. 182-3) the animal does not extend into the upper parts of the intertidal zone, lying below *Chthamalus* sp. and the main belt of *Balanus glandula*. Observations made by diving indicate that neither does it occur sublittorally; careful search in places where it is abundant in the intertidal zone has failed to reveal it on the lower parts of pier pilings, on sublittoral rocks or on reefs. Such is the case at Santa Monica, Point Dume, Latigo Cove, Topanga Canyon and Palos Verdes—all in southern California.

ORIENTATION ON THE ROCKS

Examination of groups of animals shows that over a restricted area most of the individuals have their capitula orientated in the same direction. Except in places where wave action is relatively light, it is at once evident that, in contrast to what might be expected from observations on the reactions of the cirri of operculates to currents (Southward 1955), the dominant orientation is not such as to bring

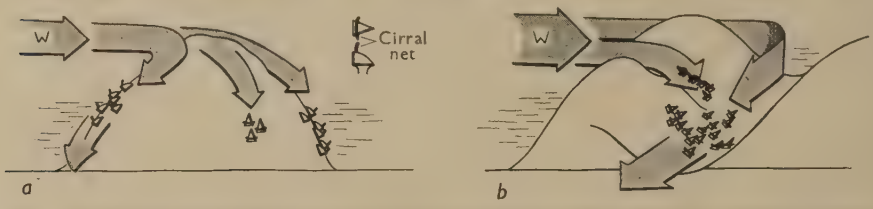
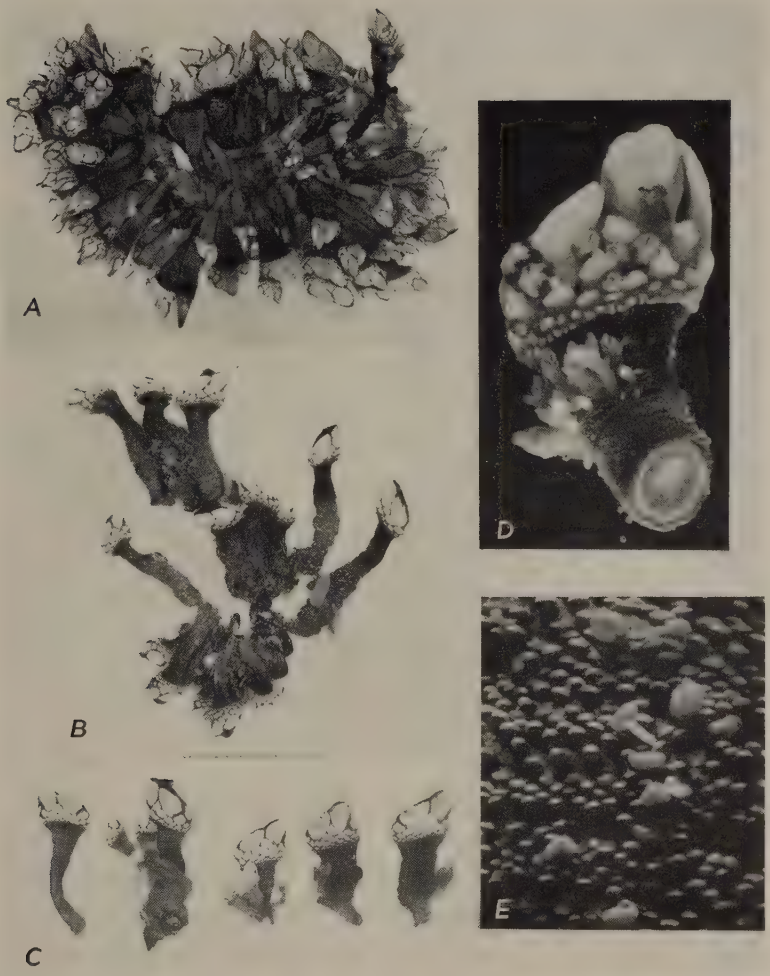


Fig. 1. Diagram to show orientation of *Pollicipes polymerus* to water flow; W = direction of wave.
(*a*) on a large exposed boulder,
(*b*) where a number of boulders have formed channels.

the anterior face of the cirral net against the incoming waves. On the contrary, it is usually such as to bring the open cirral net at right angles to the flow of water but with the anterior (captorial) face into the stream as it pours off the rocks subsequent to the breaking of the waves. The orientation is not, therefore, fixed relative to the shore-line or general wave-direction but is determined by the microtopography of each local situation, varying with any irregularities and their position with respect to the breaking waves. In general, on both the seaward and landward sides of a large boulder the capitula are so positioned that their openings are in a plane at right angles to the rock faces and in the line of run-off of the water. This is most evident in exposed situations. The anterior face of each cirral net is brought to face the rush of water, in the one case as it surges down the seaward face of the boulder after the wave has broken, in the other (at a later stage of the tide) as it flows over and pours down the landward side (Fig. 1*a*). Where there are well-marked channels, either in the rocks themselves or formed by a series of contiguous boulders, the dominant orientation is to the axis of the channel with the cirral net at right angles to it and the captorial (anterior) face directed to the current as it flows down the channel after a wave has broken (Fig. 1*b*). Animals



Pollicipes polymerus: *A*. A loose clump from a moderately sheltered site after washing away most of the debris.
B. A partially dissected loose clump showing the elongated peduncles.
C. Variation in growth form within a clump; note juveniles attached to peduncles of older animals and twisting their own peduncles to bring the capitula to a favourable position at the surface of the clump.
D. Young spat settled on adult peduncle; note absence of *P. polymerus* from capitulum on which, however, there are a number of adult *Chthamalus fissus*.
E. Cyprids and young spat orientated on adult peduncle.

(*Facing p. 170*)

Pollicipes polymerus at Point Latigo, southern California: *A* and *B*. General views showing dense aggregation and association with *Mytilus californianus*.
C, *D*, *E* and *F*. Detailed views of small areas where orientation to the dominant water flow was determined as described in text (see p. 171).

(*Facing p. 171*)

on the sides, as distinct from the floor, of such a channel, are similarly orientated but the capitulum as a whole retains the same relative position to the rock surface. Where, as a result of the micro-topography there is a general turbulent motion rather than a distinct flow pattern, then there is no dominant orientation; this is frequently the situation at the corners of a large boulder or amongst a collection of small rocks (Pl. 5*F*).

Pl. 5 shows views taken over the top of a large boulder (at Point Latigo, southern California) which has a heavy covering of *Pollicipes polymerus*, together with some *Mytilus californianus* and a little *Balanus glandula*. The tendency for animals within a restricted area to show a well-marked orientation is very evident, as is the change in this orientation from one part of the boulder to another. The orientations were measured as follows. Observations as the waves broke over the rocks allowed the main directions of flow to be determined. Photographs were then taken of several selected areas with the plane of the camera lens parallel to the rock surface; as far as possible relatively flat parts of the surface were chosen. Even when the surface is curved, distortion over a small area will not seriously affect the results. On each photograph the angle of the opening of the capitulum to the line of flow of the water, as determined from previous observations, was measured for twenty to forty randomly selected individuals. An animal with its cirral net at right angles to the current and with its anterior face pointing upstream (*i.e.* with its carinal end downstream) is considered to lie at 180°. The shape of the capitulum allows these angles to be readily determined even though the cirri are not extruded. The orientation angles (0-360°) were then treated as vector quantities, resolved, and summed and the mean values calculated. This method has been used (Barnes, Crisp & Powell 1951, Crisp & Barnes 1954) in studying the orientation of cyprids to light and surface contour. If ϕ_i is the orientation of the ith individual then the mean component (A) along the current is $\Sigma_i (\cos \phi_i)/N$ and the mean component (B) across the current is $\Sigma_i(\sin \phi_i)/N$, where N is the number of individuals. The mean direction is given by $\tan^{-1}\theta = B/A$; the resultant, $R = \sqrt{A^2+B^2}$ is, together with the sample number, a measure of the strength of the orientation. For a randomly orientated population A, B and R, approximate to zero, while θ may have any value according to the chance direction of sampling errors; if orientation is real, θ will differ significantly from zero and R gives a measure of the strength and, in conjunction with the sample number, the significance of the value of θ. For a complete orientation, $R = 1$.

Pl. 5*D* shows details of an area forming a small part of the channel leading over the face of the boulder; here $\theta = 178°$ and $R = 0{\cdot}95$ ($N = 42$) and clearly the dominant and significant orientation is close to 180°. Pl. 5*E* and *C* show animals that are likewise well orientated; for these $\theta = 185°$, $R = 0{\cdot}89$ ($N = 35$) and $\theta = 187°$, $R = 0{\cdot}90$ ($N = 27$), respectively, so that both show the form of orientation described above. By contrast the region of Pl. 5*F* is one of high turbulence and the absence of any dominant orientation, evident from the photographs, is confirmed by the measurements which give $\theta = 286°$, $R = 0{\cdot}27$ ($N = 27$); little significance can be attached to such a value of θ.

(*a*) *The origin of the orientation*

It has been shown that *Pollicipes polymerus* has no regular cirral beat; in its macro-feeding activity food is carried to the mouth after appropriate stimulation of the individual cirri (Barnes & Reese 1959). In the absence of a rhythmical beat the orientation with respect to water currents described above is an effective adaptation that ensures a favourable position for feeding activity. When the anterior face of the cirral net is at right angles to the dominant water flow then both the maximum chance of contact with planktonic material and the greatest efficiency in its transport by the cirri to the mouth parts are ensured. It is not clear, however, why this leads to the anterior face of the cirral net being directed to the back rush of water rather than to the incoming waves. The following explanation is suggested: it will be shown below (see p. 174) that a certain amount of general water movement is essential before more specialized responses are readily evoked. Under natural conditions it would seem that this initial level of

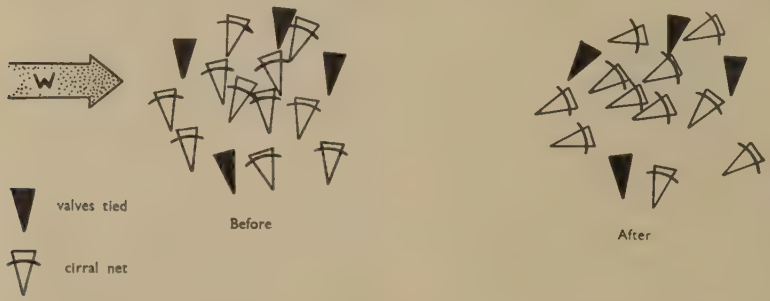


Fig. 2. Diagram to show change in orientation of selected individuals from a group of *Pollicipes polymerus* caused by directional flow of water. The water flow (W) was 1 l. per 6 sec from two jets 12 mm apart and of 5 mm bore situated 12 cm from the leading edge of the group of animals; duration of experiment 24 h. Note that the animals at the leading edge orientate unless the capitulum is tied (see text p. 173).

activity is initiated and then in part maintained by the incoming waves, the animal then being in a more favourable state to respond subsequently to directional water currents, the first of which to reach it will be those following the breaking of the wave and often consisting of the back rush of water as it flows down the rocks.

Animals may be maintained for quite long periods in the laboratory in a healthy and actively feeding condition; this is best done by playing a continuous jet of water over the animals while maintaining them under running water, rather than by stirring or by bubbling with air. If such a jet is directed laterally on to the cirral net of an active animal it slowly turns so that the anterior face of the cirri is brought towards the jet. This orientation is not brought about by a temporary twisting of the cirri alone but by a slow turning of the whole capitulum. If the jet is directed at the peduncle no turning takes place, although with a strong jet the peduncle may bend towards it. These experiments indicate that although the receptors are situated in the cirri, the ultimate response is in the musculature of the peduncle. This is supported by the fact that if the capitulum is tied

with a piece of twine, no turning response is obtained to a jet of water; under these conditions, however, it is evident that there is an effort to open and the twine may be considerably stretched; receptors responding to general water movement rather than directional flow may, therefore, be present in the peduncle. When the twine is removed, the capitulum opens, the cirri are extruded and the turning response takes place. With an isolated animal this turning response is easily obtained; under the influence of a moderate jet directed at the side the capitulum will slowly turn through an angle of 90°. To obtain the response under laboratory conditions from a whole group of animals and thereby simulate conditions on the shore is more difficult; the reasons for this are twofold. First it is difficult to obtain and then maintain a strong enough water flow whose volume is adequate to cover the whole group, and secondly, the general activity of experimental animals is much more variable than is the case when they are subjected to vigorous wave action together with uni-directional flow. Fig. 2 shows the orientating effect of a stream of water played over a small group of animals for several hours; clearly the individuals nearest the jet have responded in a manner similar to isolated individuals. Those animals somewhat further away from the jet have shown partial orientation but there is little response from the animals furthest away from the jet which have been partially shielded by other animals and subjected to the least current intensity. Most of the animals in which the capitulum had been tied gave no response. In one case, however, there was considerable bending of the peduncle rather than the normal twisting response; this is a response of the peduncle to pressure and not mediated through the cirri; it may be elicited by mechanical or electrical stimulation of the peduncle.

Although this evidence strongly suggests that the effective receptors that initiate the turning response are present in the cirri, it is difficult to be certain that this is the case. Under a vigorous flow of water and with a fully active animal the body is freely exposed to water, being raised in the mantle cavity; it is possible, therefore, that the receptors lie in the body surface. Experiments in which a fine jet was directed at the cirri tend, however, to negate this suggestion, for under these conditions the body is largely protected from the impact of the water by the valves and yet the response is still obtained. Attempts were made to resolve the problem by observing animals in which one or more of the cirri had been cut off; the animals did not, however, behave normally and the results were inconclusive. There are nerve endings at the base of the spinous processes of the cirri and these may be directly involved in the response; whether these receptors are identical with those responsible for the 'feeding' responses of the cirri to touch is not known. We have little information on sensory receptors in the cirripedes, but sensory receptors in the bristles of other crustacean appendages are well known (see for example, Laubmann 1912, Wetzel 1935). Since a different response is obtained it seems probable that a different set of receptors is involved. On the other hand by analogy with other animals the response may be in stretch receptors, possibly situated at the base of the cirri, and activated by the bending of the cirri under water pressure. Stretch receptors have recently been described by

Wiersma (1959) in representative species of all four groups of the Crustacea Decapoda.

This response to uni-directional currents recalls the behaviour of some operculates. Moore (1935), who first called attention to the curvature sometimes found in the radial canals of the basis of *Balanus perforatus*, pointed out that this could have taken place by rotation of the barnacle about its vertical (dorso-ventral) axis during growth. Crisp & Stubbings (1957) have shown that many species, particularly when young and growing actively, will twist in response to uni-directional currents so as to bring the anterior face of the cirral net to beat into the current; the phenomenon is not, as suggested earlier by Crisp (1953) restricted to those species with a calcareous base. A temporary rotation to currents is shown by many barnacles although the intensity of the response seems to vary from species to species and to be related to variations in the normal habitat conditions. It is again evident that the response is mediated through the cirri; if a lateral jet is directed at a closed animal then the cirri emerge normally but slowly twist to face the current. The ultimate twist of the whole animal during its growth was explained by Crisp (1953) on the assumption that continuous twisting in a given direction will give rise to differential growth-rates according to whether the growing point is subjected to compression or tension. These pressures must be transmitted via the operculum since the muscles moving the thorax to which the cirri are attached are not, as stated by Crisp, attached to the basis.

In *Pollicipes polymerus* the reception of the stimulus by the cirri is believed to be followed by integrative action and orientation achieved by rotation of the whole capitulum by means of the muscles of the peduncle; the rotation is essentially, therefore, 'temporary' and whilst it may be virtually maintained in positions where uni-directional currents are of constant occurrence, it does not become fixed as in an operculate. This would seem to have considerable advantage in situations where, although due to local micro-topography the water flow is dominantly uni-directional, minor changes result from variations in the angle of approach of the waves; adjustments of the cirri can readily be made to such minor changes.

(*b*) *The reactions to non-directional currents*

When a group of animals still attached to their substratum is observed in still water, either in the field or in the laboratory, they show little sign of activity; from time to time the valves open and the cirri are partially extruded. There is no macro-feeding activity and indeed the cirri are, under these conditions, rarely expanded sufficiently to feed effectively. If the water is stirred vigorously the activity of the animals is increased; the valves open more widely and the cirri may even be fully expanded. When a vigorous jet of water is directed at the animals the capitulum opens, the cirral net is held stiffly out and food, if available, is readily taken. The behaviour is similar on the shore; as the tide rises and water reaches the animals the cirri are first protruded and hang out somewhat limply between successive waves. With increasing exposure to wave action the cirri

become fully expanded and activity of the stalk in the form of bending movements often takes place. It is very evident that for effective cirral response to various forms of stimulation a considerable amount of water movement must be present to maintain a 'basal' activity.

(*c*) *Orientation at settlement*

It has already been pointed out that solitary individuals are rather rare. Furthermore, neither cyprids nor young spat (which are more easily detected) are found in numbers on the rocks. By contrast, the peduncles of adults, both small and large, are covered with cyprids and young spat at the breeding season (Pl. 4 *C* and *D*). This would seem to be an extreme case of the gregarious behaviour shown by some operculate species (Knight-Jones 1953, 1955). This author has contended that species recognition is often involved and, if this contention be upheld, this could well be the situation in *P. polymerus*. On the other hand, the restriction of settling to the adult peduncle may only reflect specialized demands on the part of the cyprid with regard to the character of the actual settling surface. It is well known that not only do cyprids settle in greater numbers on rough surfaces but also that they are very sensitive to surface contour (Crisp & Barnes 1954, Barnes 1956 a, b). In particular there is a marked preference for pits and grooves, in the latter the cyprid being dominantly orientated along the line of the groove. The epidermis of the peduncle of *P. polymerus* is rough and, moreover, the presence of the closely packed and symmetrically arranged calcareous scales gives rise to a series of regular interscalar areas equivalent to depressions or pits which are of a size comparable to that of the cyprid. It is in these small interscalar grooves and aligned with their long axis that the cyprids and young spat are found (Pl. 4*E*). Subsequent to settlement the newly developing peduncle twists so as to bring its small capitulum into a favourable position in relation to its neighbours and water currents and, although the orientation of the capitulum itself to the elongated interscalar depression is then lost, the attachment of the peduncle within this area is still clearly evident.

It is a curious fact that this restriction to the adult as a settling surface is virtually limited to the peduncle; very rarely are cyprids found on the capitulum even between the calcareous plates. This is in marked contrast to other species, particularly *Chthamalus* sp. and also to some extent to *Balanus glandula*, which are commonly found on the capitula of *Pollicipes polymerus* and, as might be expected, in particular in the cracks and grooves between the valves (Pl. 4*D*). If specific recognition is involved then it must be to some specific property of the peduncle that the free-living cyprids react.

SPONTANEOUS ACTIVITY

Inherent spontaneous activity under constant conditions of the environment is now known to occur in some invertebrates (Batham & Pantin 1950 a, b). Such activity is often of a very simple character such as changes of shape, for example, in *Metridium senile*, and the pattern of activity varies in character from one

animal to another; these different patterns are usually termed phases. The phases often alternate with one another so that the activity assumes a roughly rhythmical character which does not appear to be the result of variations in the environment; it seems to be entirely endogenous and there is a tendency for alternating changes of phase without any external stimulation.

Observations have been made on certain types of inherent activity, in particular opening movements of the valves and changes in the peduncle, in *Pollicipes polymerus*. The experimental methods were similar to those of Batham & Pantin (1950 a, b), namely direct observation, time-lapse photography and kymograph recordings. For the last, light isotonic levers were used. The animals were collected from mid-tide level on the day of the experiment and before use were kept in

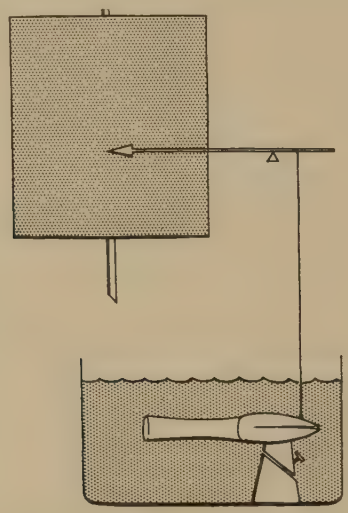


Fig. 3. The method of mounting *Pollicipes polymerus* and attaching the string to record opening movements without interference by peduncular movements.

moist cotton wool or still water; usually about 2 hours elapsed between collection and the beginning of an experiment. Investigations were made with the animals in air and in water as well during the transition from one medium to the other. Occasionally the experimental animals were still attached to stones or mussel shells, but more often they were first carefully detached from the substratum; damaged animals in which there was any sign of escape of the peduncular fluid were not used. During an experiment the animals were mounted as described below and kept in a dish which protected them from air currents. The room was relatively free from vibration and disturbances and, although not thermostatically controlled, remained at a roughly constant temperature (checked at intervals) throughout a run. In the early experiments an attempt was made to record

movements simultaneously from several points on the peduncle and from the capitulum. With this arrangement, however, the results were difficult to interpret; in particular it was impossible to separate the small opening movements of the two halves of the capitulum from those of the peduncle. Movement of the latter was, therefore, recorded by means of a single string attached at the junction of the peduncle and capitulum. Such records, unless supplemented by direct observations, do not indicate either the true direction or type of stalk movement, whether bending or simple contraction; records of this kind were taken on the same drum simultaneously from several animals. Even when strings are attached only to the capitulum, the records do not allow its opening movements to be separately determined; for these the following experimental method was used (Fig. 3). The intact animal was fastened at one side to a small piece of cork using a quick-setting glue; another piece of cork, cut to take the first, was glued securely to the bottom of a glass vessel and the two corks secured by a stout pin. A light string was attached to the upper free half of the capitulum of the animal and lead to the recording lever. In this way only the movements of the free half of the capitulum are recorded and they are virtually independent of any movement of the peduncle. The mechanical advantage of the system with respect to opening movements will be particularly affected by the exact point of attachment of the string. This was not always the same, since it was thought more desirable to reduce the time between collection of the animals and the beginning of an experiment rather than aim at precision in positioning the attachment of the string; the appropriate measurements were, however, made so that actual movements could be subsequently calculated. In order to keep the air around the peduncle moist some water was always kept in the bottom of the container. When determining the effects of transfer from one medium to another the sea water was always temperature-equilibrated with the air.

The opening movements will be considered first. Figs. 4 and 5 show representative kymograph records taken from the capitulum with the animal in air and sea water; several kymograph speeds were used and in all cases the upstroke indicates closure of the valves. Fig. 4*a* is a record of almost 4 h continuous activity. The first part of the record (up to A) when the animal was in air, shows not only major opening movements but also between them frequent small pulsations. The activity is by no means rhythmical; nevertheless, there is continued activity with repeated major movements about every 15-20 min; these movements correspond to the opening of the capitulum (Pl 6). Whilst the latter is open there are frequently a series of smaller movements which may be termed pulsations. The latter although registered as opening movements may not originate in the muscular activity of the capitulum *per se* but may arise from movements of the body and cirri within the mantle cavity, such movements being transmitted to the capitulum to which the body is attached. It is evident from the records, particularly those run at the higher speeds (Fig. 4 *b* and *c*), that whereas closure is a rapid and smoothly continuous movement, opening is less so; during the first part of the latter the movement is rapid and almost as fast as the closure, but this is followed by successive

jerky movements. This is in agreement with what is known of the mechanism of the movements. Closure is effected by the large adductor scutorum muscle but opening involves movement of the body. Furthermore, in water opening may be

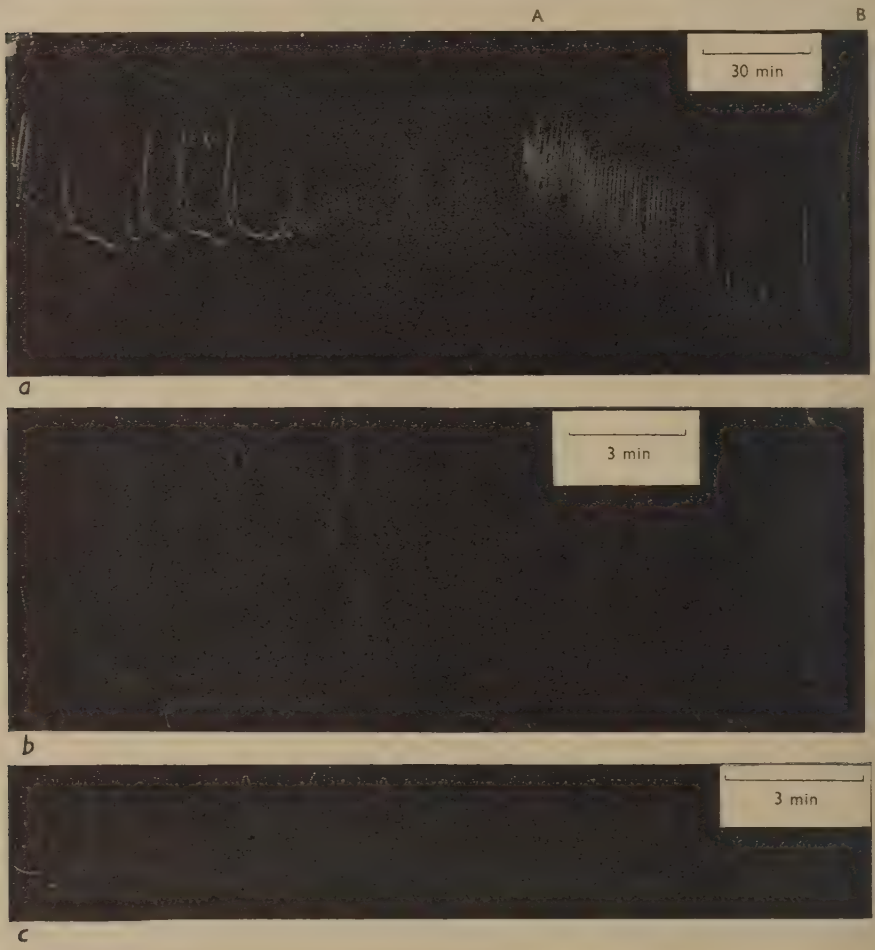


Fig. 4. *Pollicipes polymerus*, various kymograph records:

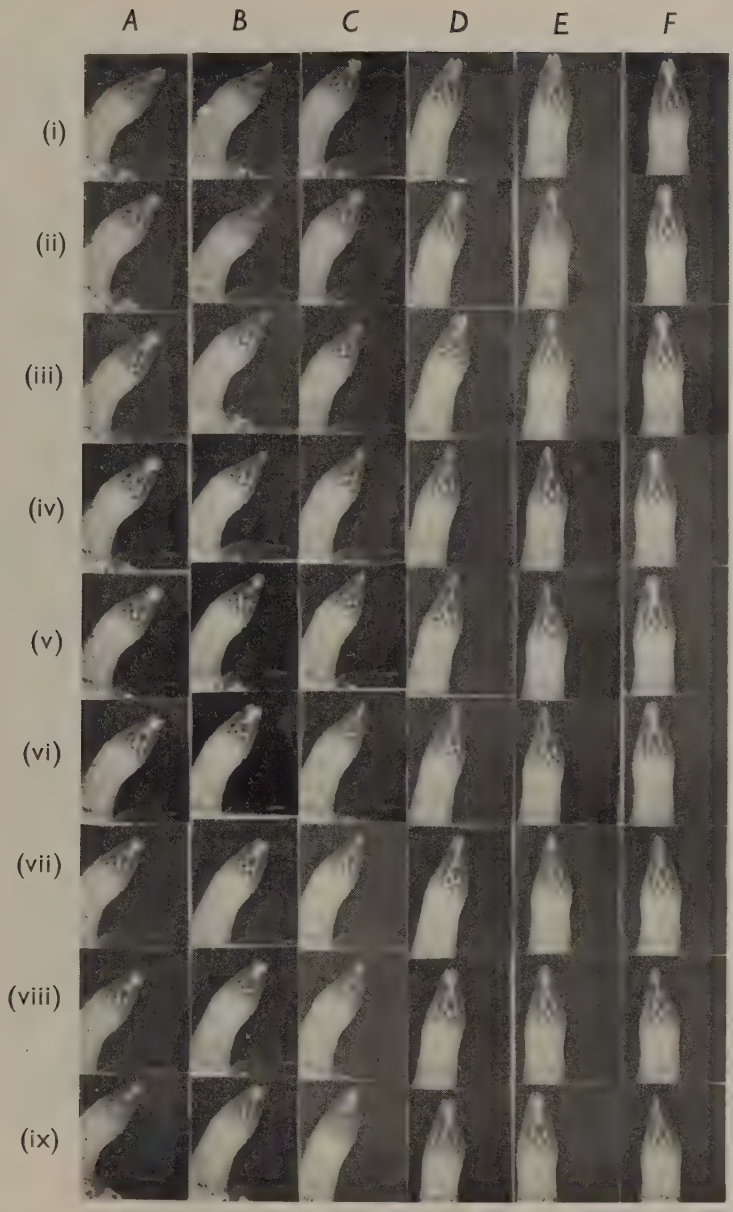
a, Record from the capitulum; the animal was in air for 2 h 25 min (up to A), when sea water was added; the valves were closed at the end of the experiment by mechanical stimulation (B).

b, Record from the capitulum of an animal in air throughout the experiment. The lower record follows the upper after an interval of 2 h. A record was only taken for a limited period during the experiment.

c, Record from the capitulum of an animal in water throughout the experiment; a fast drum speed was used.

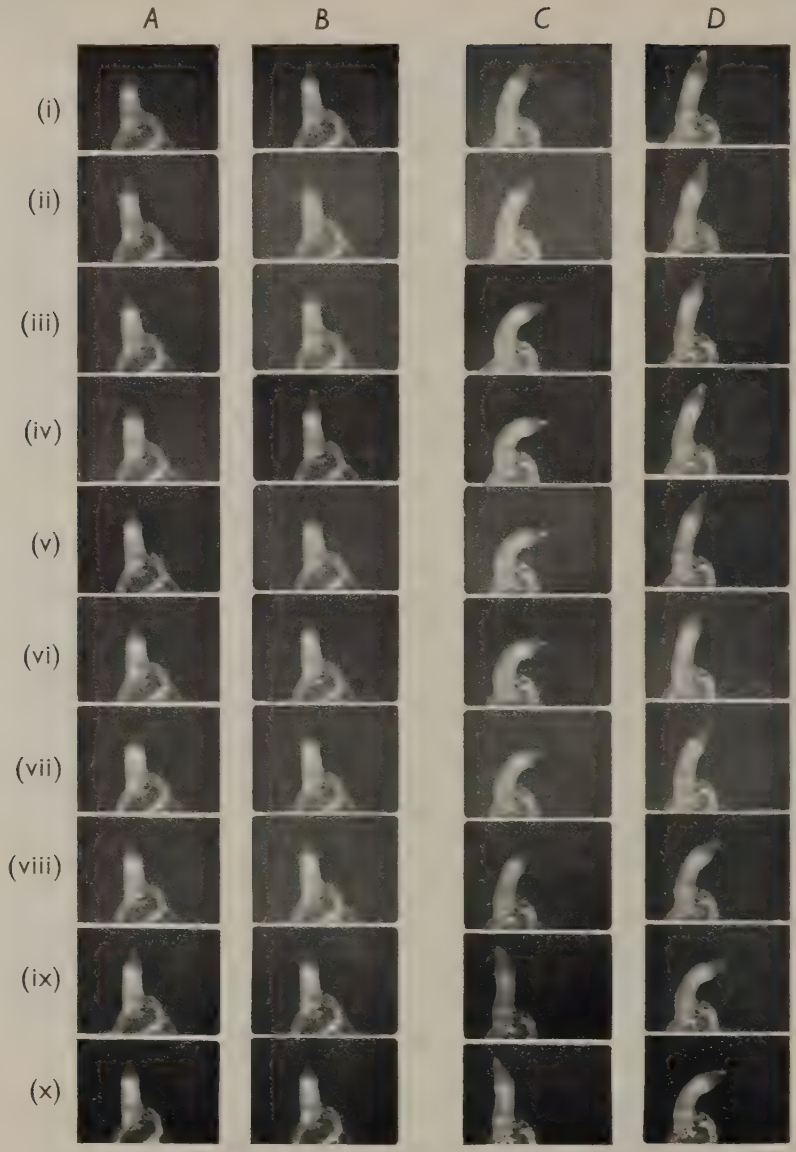
followed by partial extrusion of the cirri whose withdrawal may or may not be accompanied by closure of the capitulum itself.

Whereas in air the movements are at relatively long intervals, on transition to water (Fig. 4*a*, at A) they become much more frequent, about every 1-2 min and



Pollicipes polymerus: time-lapse photographs showing opening movements printed directly from film strip, 5 sec intervals between each shot. Note the rapidity of closure, *D*(iii)-*D*(iv), compared with opening *D*(vi)-*E*(i); even in the 'closed' position the mantle cavity is still in communication with the outside by means of a small and adjustable aperture, *B*(iv), *C*(iv), *D*(iv) and *E*(iv).

(*Facing p. 178*)



Pollicipes polymerus, time-lapse photographs: *A* and *B*. In air at 40 sec intervals. Movement here is largely expansion and contraction of the peduncle; contrast, for example, *A*(vi) and *B*(vii).
C and *D*. In sea water at 2 min intervals showing bending, some contraction and rhythmical movement of the valves (see *D*(iii), (iv), and (v)).

(*Facing p. 179*)

much more regular, although the form of the movements is the same. Eventually, however, the movements decrease in amplitude and frequency, and this may probably be ascribed to reduced viability under the laboratory conditions.

The frequency between successive opening movements both in air and water, have been determined from all the records and the results, grouped into frequency classes, are shown in Fig. 6. Only the major movements have been considered and the selection must be to some extent arbitrary. It is evident that in water there is a distinct aggregation of the values round 50-100 sec, and since this peak is relatively well marked, the movement can be considered to approximate to rhythmical. In air, however, the frequencies spread over a wide range, up to 1000 sec, and there is little evidence of a dominant frequency: as far as this analysis allows any conclusion to be drawn it must be considered that this periodic movement shows little approach to a regular rhythm. In both air and water, however, the animals show continuous inherent activity which exists under constant conditions of the environment.

Fig. 5. *Pollicipes polymerus*: a kymograph record of peduncle activity in air. The string was attached to the peduncle just below the capitulum; no distinction is possible between contraction and bending; the record shows continuous activity for 8½ h.

The maximum movements in air of the centre of the occludent edge of the scutum lie between 0·5-1·0 mm for a moderate-sized animal, so that if both halves of the capitulum were free to move they would separate at this point by double this distance. It should be emphasized that this does not necessarily mean that an aperture of that width leading into the mantle cavity is present. The size and shape of the opening when the animal is in air seems to be ultimately under control of the fold of membrane underlying the scuta rather than the movement of the whole valves; the complicated musculature of this membrane was commented upon by Darwin (1851) who did not, however, give any suggestions regarding its function. In water, when the cirri are not extruded, the movements are of a similar amplitude to those in air. However, it must be stressed that in water the 'zero' position about which such movements take place is different; it is about a partially opened position. This is evident from a comparison of the amplitude obtained for total closure when the animal is artificially stimulated.

These movements of *P. polymerus* recall those described for an operculate, *Balanus balanoides*, when exposed to air (Barnes & Barnes 1957) and the above

experiments were, therefore, supplemented by direct observations on the animals in air and water under a low power binocular microscope. The results amply support the kymograph records and confirm the similarity of behaviour to *B. balanoides*. When animals are transferred from water to air the capitulum is at first open widely and the cirri are extruded but not expanded. Repetition of these movements clears most of the water from the mantle cavity very quickly. These movements decrease in frequency and intensity but then over an extended period,

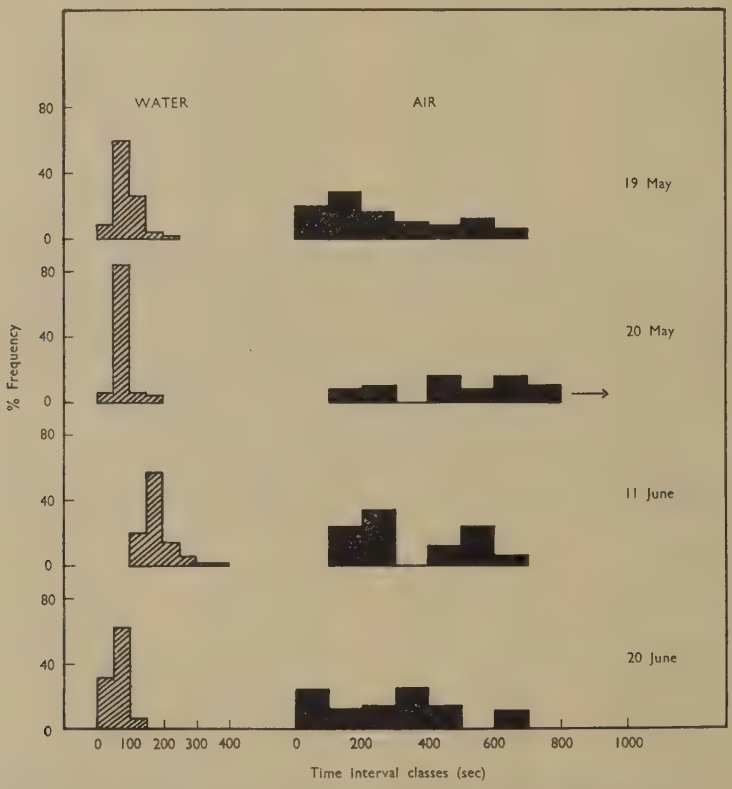


Fig. 6. *Pollicipes polymerus*: the frequency of major opening movements in air and water. The pooled results from several groups of animals on different days are shown; different animals were used in air and water.

which corresponds to the kymograph records, there are movements that put the mantle cavity into direct contact with the air. During this period the capitulum is rarely tightly shut, as is the case when it is touched, and the size of the entrance to the mantle cavity is seen to be regulated by the tissue underlying the valves. Occasionally, however, the capitulum is closed more tightly and a small drop of water may then be extruded. That the mantle is full of air under these conditions is clearly evident when the animal is transferred to water; the capitulum is

opened and bubbles of air escape from the mantle cavity. This is followed by continuous activity.

ACTIVITY OF THE PEDUNCLE

In either air or water the peduncle undergoes changes of shape—retraction, expansion—as well as bending movements. In water these movements although sluggish are often quite readily seen, and are shown in Pl. 7 *C* and *D*. In air they are less obvious but become evident from kymograph recordings (Fig. 5) or time lapse photograph (P. 7 *A* and *B*). The kymograph record shows the frequency and amplitude of the movements to decrease with time as the animal tends to dry out. Continued exposure to air over a period of more than 6 h is unnatural and not experienced under the normal habitat conditions. The activity can hardly be said to be rhythmical but it is continuous and varies considerably with the size and state of the animal.

GROWTH

Batham (1945) found that growth in *Pollicipes spinosus* is extremely slow and that sexual maturity was only reached after about 5 years. The same is true for *P. polymerus*. A number of measurements have been made on marked individuals at Point Dune, California, where the exposure is considerable and conditions are very favourable for the species. The distance from the apex of the tergum to that of the carina was measured. During the course of 16 months the mean size for ten individuals increased from 17·8 to 18·5 mm, and of another set of nine individuals from 12·1 to 12·6 mm. This is an extremely slow growth-rate, and very similar to that of Batham's specimen V (1945, Table 1) which increased from 17 to 18 mm in 2 years. Since large animals may measure 20-25 mm, and since growth-rate while faster in the smaller animals will decrease with age, Batham's estimate of 15 years to full size may well be an underestimate; fully grown animals may be 20 years old.

Examination of a large number of animals has shown that they never contain egg lamellae below a size of 10-11 mm. This again agrees with Batham's observations, and, bearing in mind the similarity of growth-rates in the two species, it may be assumed that in *P. polymerus* maturity is not attained before the fifth year.

DISCUSSION

An attempt may now be made to relate the observations on the behaviour of the animal as observed both in the field and under experimental conditions, to the salient features of its distribution in the littoral zone. It must, however, first be stressed that as with other sedentary animals whose larvae are planktonic, there is always the problem how far the distribution is to be ascribed to the behaviour of the planktonic as distinct from that of the sedentary phase. On the one hand, the adult distribution may be considered to be the result of the action of environemnt on adults subsequent to a more or less indiscriminate settling behaviour on the part of the planktonic larvae; indeed, as regards sublittoral species, this was once

the dominant view. On the other hand, while there may well be a lack of discrimination in settlement in some species, more and more evidence is accumulating that in many species only 'suitable' sites are 'selected' by the larvae, and often the behaviour of the spat at settlement and just before metamorphosis is such as to favour sites which are well adapted to the adult animal. We have little knowledge of the behaviour of the cyprids of *Pollicipes* as regards their distribution at settlement, and any interpretation must therefore be tentative. There is no direct evidence with regard to their distribution within the littoral zone and below low tide level. By analogy with other intertidal species it might be expected that they would tend to remain in the upper water layers and that settlement would be greatly influenced by wave action. There is little doubt that settlement is heavy amongst adults of the same species. Whether species recognition is involved in this behaviour or whether it is only specialized requirements of the surface texture that are met most commonly by the surface of the peduncles of adults, is not known. In any event the phenomenon is clearly responsible for the maintenance of dense masses of the animal in suitable places. It is usually considered that in operculates, where the phenomenon of gregarious behaviour has been studied, the biological significance of such behaviour is largely to ensure the proximity of individuals; in species in which, although hermaphroditic, cross-fertilization is obligatory, breeding may then take place. There is evidence, however, that in *P. polymerus* self-fertilization is the rule, and unless the phenomenon is regarded as a relict (in the evolutionary sense) this explanation is inadequate. *Pollicipes* although not now regarded as the ancestral cirripede stock is certainly a very ancient genus, in which self-fertilization may have been expected. However, self-fertility may have been secondarily developed and gregarious behaviour a relict of an obligate cross-fertilizing phase. On the other hand it may be noted that most pedunculates are deep water animals and that even in those species where dwarf males have been developed and contiguity of adults is not essential for breeding, settlement of young spat on the peduncles of adults is often marked. In deep water, surfaces available for settlement are comparatively rare and such gregarious behaviour involving rapid settlement may not only be an adaptation to ensure contiguity but also to ensure that the available surface provided by adult peduncles is colonized; such an adaptation could be carried into the intertidal habitat. The response is of course another example of rugophily which has been shown to be a common feature of the cyprids of many other species (Crisp & Barnes 1954). Apart from the advantages discussed above, settlement within a pit, formed in this case by the interscalar areas of the peduncle, has the advantage of providing a good 'key' for attachment.

There is possibly some survival value in the aggregative behaviour in the case of *Pollicipes* in providing shelter from abrasion and predators and perhaps from excessive desiccation while the animals are still young. The species is very slow growing and the small and delicate stages being, therefore, prolonged, any such protection is of importance. The formation of dense aggregates in intertidal operculates may lead to wholesale destruction of the adult population, particularly

at low tide levels (Barnes & Powell 1950). In a slow-growing species such as *P. polymerus*, which takes several years to reach sexual maturity and in which the aggregative behaviour leads to dense masses of the animal, the capacity of the peduncles to adjust themselves in relation to their neighbours and yet for each to bring its capitulum into a satisfactory position for feeding activity is of prime importance. Furthermore, this possibility of adjustment, absent in an operculate with its calcareous shell, allows the formation of a community with the mussel, which might otherwise smother the barnacle.

The restriction of *Pollicipes* to places with wave action is clearly related not only to the necessity for a certain general stimulation, which may be regarded as an extended form of its phasic behaviour, to initiate activity, but also to the mode of macro-feeding, once this level of activity has been reached (Barnes & Reese 1959); the ability to respond to uni-directional currents by a twisting of the peduncle allows full advantage to be taken of local macro- and micro-topography in feeding activities. The fact that the animals are orientated to the run-off of the waves over and between boulders rather than to the initial breaking of the wave permits of a longer feeding time; the initial breaking of the wave takes a much shorter time than the subsequent run and this is fully exploited in the feeding activity. In quiet places such as protected bays or harbours as well as in the sublittoral the necessary stimulation is absent. We have less information regarding the factors limiting the species at the upper level of the intertidal zone. Two important factors may be suggested. First, since rather specialized conditions are required for full feeding activity, and since these conditions even in the most favourable sites are only completely satisfied during a limited part of the tidal cycle (optimal only from the time the tide reaches the animals to when they are completely covered) this period, at the upper levels of the shore may be insufficient to sustain adequate growth. Secondly, desiccation at the upper tidal levels may be too severe for both spat and adults; as in intertidal balanids, adjustment of the entrance to the mantle cavity takes place but in an operculate water is lost from the peduncle and over such loss the animal has only a limited control achieved by peduncle contraction so reducing the exposed surface. It seems unlikely that competition limits the upward spread; this would have to come from *Balanus glandula* and it is difficult to see how this species, in view of the 'adjustments' of the peduncle in *Pollicipes polymerus* could successfully prevent the upward penetration of the latter.

Over the greater part of the west coast of North America the distribution is typically as has already been described. There is one notable exception and this provides an interesting test of the reliability of the ideas just discussed concerning the behaviour and distribution. The waters of the San Juan Archipelago are protected, and compared with the outer Pacific coast, wave action is very light. *P. polymerus* might be expected to be absent; this is not, however, the case. The species is not as abundant as on the outer coasts, and rarely forms dense masses on vertical faces of rock. In parts of the coast, however, owing to the nature and configuration of the rocks, the steep cliffs are often cut by gullies that may extend well above high tide level. It is in such gullies that the pedunculate is most

common, where it may form quite dense masses that are particularly well orientated as previously described to the direction of water flow down the gulley. With moderate or even light wave action observations show that the breaking waves are channelled with some force up such gullies to give a directional return stream of water. Turbulent conditions and water flow are adequate for *Pollicipes*. Furthermore, with the water channelled in this way, a band of animals within the gulley often extends over the whole intertidal region so that at the upper end of the gulley *Pollicipes* is present right across the levels occupied by *Balanus glandula* and *Chthamalus dalli*, and even to higher levels to which none of these species extend on the open rock faces. But for these specialized adaptations to a restricted part of the intertidal zone and the occurrence within the zone only where conditions are optimal for these adaptations it would seem that the slow-growing slow-maturing species could not survive.

ACKNOWLEDGMENTS

Acknowledgment is due to Professor T. H. Bullock and Dr D. L. Ray for generous help and advice during the course of this work.

SUMMARY

1. The stalked barnacle, *Pollicipes polymerus*, occurs often in dense masses in the exposed midlittoral of the American west coast.

2. The animals are orientated on the rocks so that the cirral net faces the rush of water after the waves have broken and as they pour over the rocks and boulders.

3. The orientation appears to be mediated through the cirri; comparison is made with the twisting movements of operculate barnacles.

4. Activity to non-directional currents is discussed; a certain level of current flow or turbulence is required before normal feeding activity begins.

5. The spat, which settles largely on the peduncles of adults, is orientated within the pits formed by the calcareous scales.

6. Spontaneous activity of valves and peduncle is demonstrated. The former consists of opening and closing movements and the latter of bending, contraction and expansion. This inherent activity occurs in air and water.

7. The animals grow very slowly: some of the largest individuals may be 20 years old. Maturity is only reached after 5 years.

8. It is shown that the specialized behaviour allows the species to maintain itself in a restricted part of the intertidal zone against competition from faster-growing animals that mature quickly and produce large broods of young.

REFERENCES

Barnes, H. (1956a). Further observations on rugophilic behaviour in *Balanus balanoides* (L.). *Vidensk. Medd. dansk naturh. Foren. Kbh.* **117,** 341-8.

Barnes, H. (1956b). Surface roughness and the settlement of *Balanus balanoides* (L.). *Arch. Soc. Zool.-bot. fenn. Vanamo,* **10,** 164-8.

Barnes, H. & Barnes, M. (1957). Resistance to desiccation in intertidal barnacles. *Science,* **126,** 358.

Barnes, H., Crisp, D. J. & Powell, H. T. (1951). Observations on the orientation of some species of barnacles. *J. Anim. Ecol.* **20,** 227-41.

Barnes, H. & Powell, H. T. (1950). The development, general morphology and subsequent elimination of barnacle populations, *Balanus crenatus* and *B. balanoides*, after heavy initial settlement. *J. Anim. Ecol.* **19,** 175-9.

Barnes, H. & Reese, E. S. (1959). Feeding in the pedunculate cirripede *Pollicipes polymerus* J. B. Sowerby. *Proc. Zool. Soc. Lond.* **132,** 569-85.

Batham, E. J. (1945). *Pollicipes spinosus* Quoy and Gaimard. I. Notes on biology and anatomy of adult barnacle. *Trans. Roy. Soc. N.Z.* **74,** 359-74.

Batham, E. J. & Pantin, C. F. A. (1950a). Inherent activity in the sea anemone, *Metridium senile* (L.). *J. Exp. Biol.* **27,** 264-89.

Batham, E. J. & Pantin, C. F. A. (1950b). Phases of activity in the sea-anemone, *Metridium senile* (L.) and their relation to external stimuli. *J. Exp. Biol.* **27,** 377-99.

Crisp, D. J. (1953). Changes in the orientation of barnacles of certain species in relation to water currents. *J. Anim. Ecol.* **22,** 331-43.

Crisp, D. J. & Barnes, H. (1954). The orientation and distribution of barnacles at settlement with particular reference to surface contour. *J. Anim. Ecol.* **23,** 142-62.

Crisp, D. J. & Stubbings, H. G. (1957). The orientation of barnacles to water currents. *J. Anim. Ecol.* **26,** 179-96.

Darwin, C. (1851). *A monograph on the sub-class Cirripedia, with figures of all the species.* London.

Knight-Jones, E. W. (1953). Laboratory experiments on gregariousness during setting in *Balanus balanoides* and other barnacles. *J. Exp. Biol.* **30,** 584-98.

Knight-Jones, E. W. (1955). The gregarious setting reaction of barnacles as a measure of systematic affinity. *Nature, Lond.* **174,** 226.

Laubmann, A. (1912). Untersuchungen über die Hautsinnesorgane bei decapoden Krebsen aus der Gruppe der Carididen. *Zool. Jb.* **35,** 140-59.

Moore, H. B. (1935). The biology of *Balanus balanoides*. IV. Relation to environmental factors. *J. Mar. Biol. Ass. U.K.* **20,** 279-307.

Ricketts, E. F. & Calvin, J. (1952). *Between Pacific Tides.* (3rd ed.) Stanford Univ. Press.

Southward, A. J. (1955). On the behaviour of barnacles, 1. The relation of cirral and other activities of temperature. 2. The influence of habitat and tide level on cirral activity. *J. Mar. Biol. Ass. U.K.* **34,** 403-34.

Wetzel, A. (1935). Über das perephere Nervensystems der Caprelliden. *Z. Morph. Ökol. Tiere,* **30,** 206-96.

Wiersma, C. A. G. (1959). Movement receptors in decapod crustacea. *J. Mar. Biol. Ass. U.K.* **38,** 143-52.

A NEW APPROACH TO THE PROBLEM OF THE OPTIMUM TEMPERATURE FOR INSECT ACTIVITY

By C. B. WILLIAMS

Ard-Insh, Kincraig, Inverness-shire.

AND

M. F. H. OSMAN

Entomology Dept., Faculty of Science, Cairo University

(With 1 Figure in the Text)

One of the problems that has always held a particular interest for ecologists is that of the optimum temperature for insect activity in the field. As until quite recently most of the work on insect ecology has been done in temperate climates, where temperatures seldom rise above, or even reach, the optimum, there has been little progress in quantitative work on this problem. During the past few years one of us (M. F. H. O.) has been trapping insects in suction traps in the

Table 1. *Regressions of numbers of insects caught on mean temperature*

	First year			Second year		
	Mean temp. (°C)	Lower trap	Upper trap	Mean temp. (°C)	Lower trap	Upper trap
September	28·0	+·036	–	32·3	+·041	+·051
October	27·9	−·063	+·061	28·4	−·023	+·014
November	22·8	+·079	+·078	24·6	−·021	+·061
December	18·0	+·102	+·104	17·8	+·149	+·202
January	16·3	+·061	+·093	–	–	–
February	21·0	+·034	+·039	–	–	–
March	21·1	+·026	+·135	22·2	+·011	+·100
April	26·0	+·001	+·067	27·3	−·017	+·052
May	28·2	−·010	+·032	30·4	−·012	+·036
June	31·5	−·001	+·009	31·4	+·024	+·003
July	33·3	−·028	−·024	31·4	−·005	−·023
August	33·6	−·008	−·036	31·4	−·042	−·019
Average	25·6	+·019	+·051	27·7	+·011	+·048
Number of months	12	12	11	10	10	10

vicinity of Cairo, Egypt, where the summer midday temperatures frequently rise above 40° C (105° F). Some of the results obtained give the possibility of a new approach of which the following is a preliminary account.

Two suction traps, one 4 ft and the other 30 ft from the ground, were worked nearly every day from 10 a.m. to 12 noon for 2 years, from September 1955 to August 1957, with the exception of January and February 1957 for both traps, and in addition, for the upper trap only, the first month, September 1955. In

4 months of the second trapping year, September to December, the traps were worked from 9 a.m. till half an hour before sunset.

From the day-to-day changes in the number of insects caught, expressed on a logarithmic scale, partial regressions were calculated for each month for several weather factors, which included the mean temperature during the trapping hours. These regressions for the Diptera are shown in Table 1, together with the mean temperatures during trapping for the same months. It will be noticed that some of the regressions are negative, particularly in the summer and autumn, and that in general the high positive regressions occur in the winter months.

In Fig. 1 the data have been plotted graphically to show the relation between

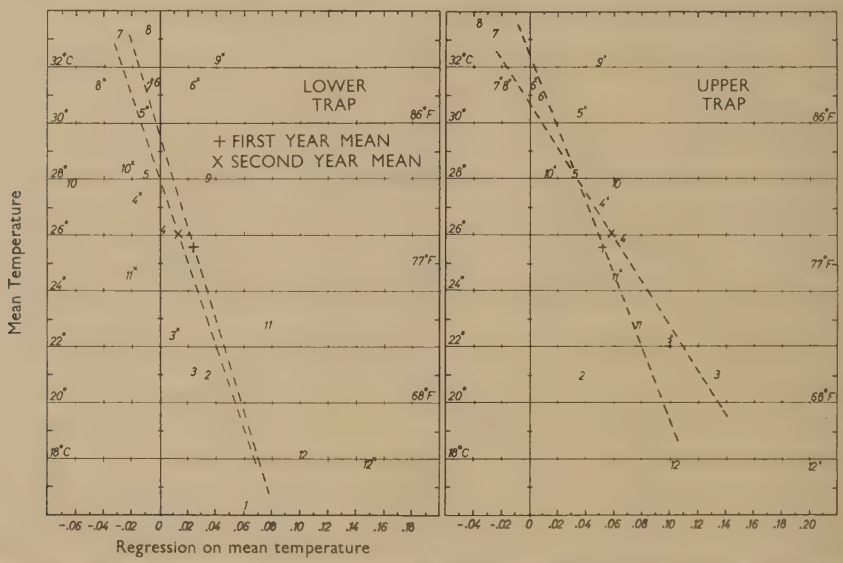


Fig. 1. The relation between the monthly regression of temperature on the log catch of Diptera (abscissa) and the mean temperature during the hours of trapping (ordinate) for insects caught in a suction trap near Cairo, Egypt, during 22 months. Also shown are the regression lines for the relation between these two, calculated for each of the 2 years, the second year with only 10 months. The months in each year are indicated by their number in the calendar year, *i.e.* '5' = May. The months in the second year are distinguished by asterisks. The lower trap was 4 ft and the upper was 30 ft above the ground.

the calculated regression for each month and the mean temperature during trapping. New regressions have next been calculated for each year and for each trap to show how the original regressions are related to the mean temperature during trapping. These are shown in Table 2. They show the rate of change of the regression of catch on temperature as the mean temperature changes from month to month during the year. They are indicated in Fig. 1 as heavy broken lines passing through the annual means. As expected, all four regressions are negative, and all cross the line of zero regression within the temperature range experienced. At these crossing points there is no effect of change of mean temperature either to reduce or increase the catch; above these points an increase of

temperature reduces the catch; below these points an increase of temperature increases the catch. The point of crossing the zero regression ordinate is therefore a measure of the optimum temperature for the activity of the Diptera under the conditions of trapping.

The approximate optimum temperatures are as follows: lower trap, first year, 29·5° C (85·0° F); second year, 28·0° C (82·5° F): upper trap, first year, 32·5° C (90·5° F); second year, 30·7° C (87·0° F). The fact that the lower trap shows lower optimum temperatures may be partly explained by the higher air temperatures near the ground during very hot days. The actual air temperatures at 30 ft are probably lower than the thermometer reading in the screen at 4 ft.

Table 2. *Regressions for each year and trap*

	First year	Second year
Lower trap	−0·00599	−0·00678
Upper trap	−0·00752	−0·01236

These results, given chiefly to indicate the method, are only for the Diptera as a whole, which are mainly small insects. Further analyses should be carried out on other orders and in other localities.

REVIEWS

A NEW JOURNAL

Field Studies. Vol. I, No. 1. Pp. 142. London: Field Studies Council. Price 5*s*. 6*d*. (post free).

Is your journal really necessary? Is it unique in bringing together papers that need bringing together, or is it a symptom of expanding output and refusal of those existing to recognize that, for practical purposes, a few large are preferable to many small journals, and to expand?

The eight papers may be placed into two, perhaps three, groups. B. J. Dresser of Dale Fort Field Centre describes how land use and farm practice in the parish of Dale depend basically on geology and climate, but have been modified by historical and economic factors. J. Oliver, University College, Swansea, describes the climate of the same area, having at his disposal consecutive observations at two main stations and information from others established for short periods to ascertain the effect of local conditions. V. J. Mercer, Juniper Hall Field Centre, gives an account of the geomorphology of the Tillingbourne. M. E. and C. D. Pigott of Sheffield University have studied the stratigraphy of Malham Tarn and the Tarn Moss.

Intermediate in character is the article by I. D. Mercer of Slapton Ley Field Centre on the Alderbury breccia. Its influence on history and land use is mentioned, but the main part of the exercise was to discover the extent to which it has been used in local buildings. Cheap in the immediate neighbourhood, it has appealed to public bodies erecting churches and schools and to a benevolent landlord housing his tenants in something more solid than wattle and daub. The author writes for others in field centres who might wish to undertake a similar project. This aim is evident also in the freshwater studies in the Shropshire Union Canal by H. M. Twigg of Preston Montford Field Centre. J. H. Barrett of Dale Fort Field Centre gives an annotated list of the birds of the parish of Dale, including Skokholm, and J. F. Morton and J. Machin of Queen Mary College, London, contribute a key to the land snails of the Flatford area. There are ecological notes and four pages of illustrations but a key cannot properly be judged except by use, which geographical considerations make impossible.

The last paper is of purely, the last but one of mainly, local interest. The canal survey is, in addition, a useful botanical survey with data on physical and chemical conditions, though there is a tendency to put forward the glib correlations of the teacher rather than the more cautious ones of the research ecologist. The list of animals is incomplete, there being identification to species in only three groups, in all of which the author has commendably sought expert help, though this prudence seems to have deserted her when she came to the Trichoptera, a group of which the larval taxonomy has not been worked out, and three species in the largest genus, *Limnophilus*, are named. The Alderbury breccia work is mainly of historical interest. The first four papers are contributions to knowledge giving no indication of origin from a place where teaching is the primary function. I think that of them only the one on the stratigraphy at Malham would have been accepted by any other ecological journal. All, however, present information of fundamental importance to ecologists; it is useful to have them together and therefore the journal passes the test set at the beginning and is to be welcomed.

There is an editorial board of six persons, of whom Prof. A. R. Clapham is chairman. The format is 12 mm narrower and 44 mm shorter than that of the *Journal of Animal Ecology* and the print is smaller. The standard of production is high. One number will

appear each year. The numerous diagrams and drawings are all of good quality but C. A. Sinker's black and white drawings of three reaches of the Shropshire Union Canal deserve special mention.

T. T. MACAN

MARINE NANNOPLANKTON

R. W. Butcher (1959). *An Introductory Account of the Smaller Algae of British Coastal Waters.* Part 1, *Introduction and Chlorophyceae.* Pp. 74; 14 plates (6 in colour). London: H.M.S.O. (*Fish. Invest.* Ser. IV.) Price 25*s*.

The algae described here are all thought to belong to the green algae, which today are commonly considered to be plants. Animal ecologists will welcome any increase in our knowledge of these small species from the point of view of nutrition and so will look forward to the publication of further parts of this work. Many small invertebrates and young stages of large ones may feed extensively on these and other algae to be described later.

The first question an ecologist is likely to ask is whether with this monograph he can identify the algae in natural populations. The work is based on the author's cultured populations and descriptions by earlier workers from natural ones. The differences likely to arise in cultures under various conditions in nature are apparently unknown. Such a study is needed if only because so much emphasis is placed on colour (p. 5) A freshwater phycologist may well disagree with the statement that 'colour, with its variations, gradations and density is perhaps the most useful of all the characters of an organism' since he will be familiar with many Chlorophyceae which can show marked variations and gradations He will probably agree with the second half of the same sentence: 'and yet it [*i.e.* colour] is one of the most difficult to represent'. He will also ask whether the representations here are accurate enough since 'in spite of attempts to get standard terms for colours it is very difficult for authors to agree on this point ... ' In the reviewer's copy *Asteromonas propulsum* is said to be 'somewhat yellow green' but is almost pure yellow in Plate VIII. *Bipedinomonas* species are 'pale green or olive green' but in Plate VIII are among the greenest depicted in the monograph. In Plates X and XI *Tetraselmis levis*, *T. verrucosa*, *T. maculata*, *T. gracilis* and *T. inconspicua* are colour pictures of organisms described as 'yellow-green', 'bright yellow green', 'rather yellow green', 'yellow green' and 'yellow green'. Neither these pictures nor the descriptions support the author's view that colour is 'the most useful of characters'. It may be doubted whether the photographs of cultured populations will help significantly in identification. Therefore, it seems that only species with very striking morphology or those described by previous authors from natural populations are likely to be identifiable from freshly collected material.

Fortunately, an extensive collection of cultures is available and these represent material of great potential value to the ecologist. The author emphasizes that he has described only 'a small portion' of these algae so that the problem of maintaining culture collections may soon become serious. Although this is not a matter considered in this work, marine biologists will soon have to consider urgently whether increased support for such collections is necessary.

J. W. G. LUND

FRESHWATER BIOLOGY

W. T. Edmondson (Editor) (**1959**). *Ward and Whipple's Freshwater Biology*, 2nd ed. Pp. xx+1248; numerous text-figures. New York: Wiley; London: Chapman & Hall. Price 276*s*.

It came as a surprise to realize that the copy of this famous book which I bought in 1931 was the original edition, copyright in 1918. Since it has been out of print for many years the issue of a second edition will be warmly welcomed. There is much (beside the price!) which is new, but it is clearly impossible to describe all the changes in a review, any more than one can presume to criticize it in detail. Suffice it to say that Prof. Edmondson seems to have succeeded to a very large extent in getting the people who really know to collaborate with him

The general arrangement is similar to that of the old edition, but the typography is considerably improved, and there are completely new sections (for example, one on aquatic fungi); others, such as the larger aquatic vegetation and those on protozoa and algae, have been completely remodelled. Others, such as the Cladocera, have changed much less, and even still contain most of the original figures.

From the point of view of the British ecologist the book inevitably still suffers from its old disadvantage that it is the North American flora and fauna which is described, but this will not prevent its being extremely useful to anyone who can afford it. Our thanks and congratulations are due to Prof. Edmondson and his collaborators.

H. C. GILSON

HANDBOOK FOR HEMIPTERISTS

T. R. E. Southwood and Dennis Leston (**1959**). *Land and Water Bugs of the British Isles*. Pp. xii+436; 32 coloured plates; 31 black and white plates; 153 text-figures. London: Warne (Wayside & Woodland Series). Price 30*s*.

There is a short introduction and key to families, an appendix on collecting and studying, a glossary, a list of plants with references to the pages where they are mentioned and an index. The rest of the book follows a uniform pattern of keys to subfamilies, genera and species and remarks on the habitat, distribution, life history, food and chromosome number of each species. There may also be comments on anything unusual about the morphology or habits, and parasites are occasionally mentioned. Half a page suffices for most species, though as many as two are devoted to some.

Most of the plates show six entire specimens and, therefore, a little more than half the total of 509 British species is illustrated. The references, at the end of each chapter, consist of author's name, date, journal, volume and pages and then a summary of the title, which seems a commendable way of saving space. References in the text are sufficiently numerous to justify the use of numbers, a practice that the reviewer generally deplores. The authors write of 'only a selection of the more important or larger works' but there seems to be nothing of importance missing from their long lists.

Readers of this journal will not rejoice to learn that, for example, *Aquarius* is no longer something to be looked for in the sky but a creature to be found upon water as well, and that, from now on, in general works they must, if they wish to be comprehensible to both young and old, write *Aquarius* (*Gerris*) *najas*; unless they deprecate this splitting of familiar genera as strongly as the reviewer does, when they will write *Gerris* (*Aquarius*) *najas*.

Hemipterists perusing this clear and concisely written book will be struck by how

much has been left out, a remark made, not as criticism, indeed a second volume by the same authors would be welcome, but because it starts a certain train of thought. How long will it be before the information in books of this kind is conveyed by means of abbreviations and symbols, as that in, for example, the Automobile Association's *Handbook* is? Data on distribution, life history and perhaps habitat could be compressed into a small compass in this way. It would, of course, require greater effort to extract the information from such a book, but the purchaser would get a great deal more for his money.

This volume will provide for the popular market a clear, well-illustrated and up-to-date account of a group for which none has been available for many years. With its full documentation it is an authoritative work which should have a good circulation in professional spheres also.

T. T. MACAN

NAMES OF LEPIDOPTERA

R. D. Macleod (1959). *Key to the Names of British Butterflies and Moths.* Pp. vii+86. London: Pitman. Price 15*s*.

The amateur naturalist is always bothered by scientific terminology and especially by the scientific names of plants and animals, so that anything which will help him to understand them is welcome. This book is the fourth of a series by the same author and adheres to the same plan. After a short introduction, there is an alphabetical list of the generic names of the butterflies. Under each genus the British species are listed and the derivation of each name is given. Following this the 'macro-moths' [*sic*] and micromoths are similarly treated.

This arrangement is far less convenient than it might sound because of the instability of generic names, which are seldom used by amateurs. To look up a specific name the reader must first know its correct generic name. The entomologist accustomed to the older editions of South's books will have a lot of difficulty. The correct name is usually to be found in the Amateur Entomologists' Society list of 1946, but even some of these names have been replaced by more recent ones. It is curiously inconsistent to be absolutely up to date with generic names, and yet to divide the lepidoptera into 'butterflies', 'macros' and 'micros', a classification as dead as the dodo.

Some may prefer the more analytical approach to the problem of scientific names provided by those books, which explain the meanings of the common Greek and Latin roots which are used as bricks in the building of new words; but there is a place for the method used here since it is particularly suitable where many of the names are fanciful or derived from mythology. A simple alphabetical dictionary of generic and specific names, including the commoner synonyms, would probably have been more convenient.

In the last ten pages selected 'common names' are listed and explained. Some have been current long enough to be truly regarded as common names, but those of the micros are of recent invention, often cumbrous and little used. They come from Heslop's list, which was compiled without reference to the well-established names of pests used by foresters and farmers. Macleod's explanation of some of Heslop's names are of historic interest.

Let no one be misled into thinking from the title of the book that it is a key to the naming of lepidoptera; as a glossary it will be useful to the keen amateur, but it is rather too specialized for general school use.

G. C. VARLEY

BOOKS RECEIVED

Ricerche sulla microfauna delle acque interne Ferraresi by MARIO F. CANELLA. Ferrara. 1954.

Studie e ricerche sui tentaculiferi nel quadro della biologia generale by MARIO F. CANELLA. Ferrara. 1957.

A Century of Biological Research. Illinois Natural History Survey Bulletin, Vol. 27, No. 2. December 1958.

Sarawak Museum Journal. Vol. VIII, No. 12. December 1958.

An Account of the Fishing Gear of England and Wales by the late F. M. DAVIS. 4th ed. London: H.M.S.O. (*Fish. Invest.* (2) XXI (8)). 1958. Price 35*s.*

The Spawning of the Plaice in the North Sea by A. C. SIMPSON. London: H.M.S.O. (*Fish. Invest.* (2) XXII (7)). 1959. Price 37*s.* 6d.

The biology and control of the American whelk tingle Urosalpinx cinerea (*Say*) *on English oyster beds* by D. A. HANCOCK. London: H.M.S.O. 1959. Price 17*s.* 6*d.*

The Wild-fowl Trust: tenth annual report for 1957-8 ed. PETER SCOTT & HUGH BOYD. Dursley. 1959. Price 10*s.*

Animal Health Yearbook, 1958. Rome: F.A.O.; London: H.M.S.O. 1959. Price 10*s.*

The Buzzard by FRANK WENZEL, translated from the Danish by REGINALD SPINK. London: Allen & Unwin. 1959. Price 35*s.*

Comparative Endocrinology edited by AUBREY GORBMAN. New York: Wiley; London: Chapman & Hall. 1959. Price 120*s.*

On the Nature of Production in the Sea by D. H. CUSHING. London: H.M.S.O. (*Fish. Invest.* (2) XXI (6)). 1959. Price 10*s.*

Machine Milking. London: H.M.S.O. (M.A.F.F. Bulletin No. 177). 1959. Price 12*s.* 6*d.*

ABSTRACTS

The abstracts are edited by Professor L. A. Harvey with the assistance in selecting and abstracting of J. D. Brayshaw, G. I. Crawford, T. A. W. Davis, A. E. Ellis, F. A. O. Fisheries Division, P. D. Gabbutt, D. Leatherdale, A. Macfadyen, J. M. D. Mackenzie, C. Matheson, E. J. Moynahan, Miss E. Nelmes, W. R. Pickering, C. D. Putnam, Mrs M. Vincent and W. B. Yapp. References are checked by B. M. Hobby. Mr R. S. R. Fitter, with the help of the societies themselves, aims to cover all the proceedings, transactions and journals of local natural history societies and field clubs. Secretaries of such organizations are urged once again to aid this work by making sure that copies of their publications are sent, regularly, to **R. S. R. Fitter, Esq., Drifts, Chinnor Hill, Oxford.** Readers and authors can materially assist by pointing out errors and omissions, and by sending reprints or offers of help in making abstracts to **Professor L. A. Harvey, The University, Exeter.**

Separate copies of the abstracts suitable for mounting on cards can be obtained from **Blackwell Scientific Publications Ltd., 24-25 Broad Street, Oxford,** or through any bookseller; price 5*s.* 6*d.* per annum, post free (issued in May and November). Back numbers of the 'Notices of publications ... ' from Vol. 3 (1954) to Vol. 20 (1951) may also be had at 2*s.* for each annual set of two parts.

CONTENTS

Note. In order to avoid unnecessary overlap with journals which the ecologist would be likely to consult in any case, papers in the *Journal of Animal Ecology* are not noticed, nor are:

(*a*) papers in *British Birds* which would fall in '4. Food and food habits';

(*b*) papers in the above journal and in *The Entomologist's Record* and *The Entomologist's Monthly Magazine* which would be classified in '5. Migration, introductions and local distribution'.

	PAGE
1. Ecological surveys and the relations of animals to habitat conditions	197
(*a*) Marine and brackish	197
(*b*) Freshwater	198
(*c*) Land	199
2. Methods, apparatus, population statistics and taxonomic studies of use to ecologists	203
3. Parasites	204
4. Food and food habits	205
5. Migration, introductions and local distribution	205
6. Studies on behaviour	209
7. Reports of organizations	211

1. ECOLOGICAL SURVEYS AND THE RELATIONS OF ANIMALS TO HABITAT CONDITIONS

(*a*) Marine and brackish

Allen, J. A. (1959). On the biology of *Pandalus borealis* Kroyer, with reference to a population off the Northumberland coast. *J. Mar. Biol. Ass. U.K.* **38,** 189-220.
The distribution of this prawn is discussed in relation to physical conditions, and a population off Northumberland is compared with others elsewhere.

Backus, R. H. & Barnes, H. (1957). Television-echo sounder observations of mid-water sound scatters. *Deep-Sea Res.* **4** (2), 116-119.
Correlation of sound echos and underwater television shows that deep scattering layers are due, not to microplankton, but to individual small fishes.

Barnes, H. & Barnes, M. (1958). The rate of development of *Balanus balanoides* (L.) larvae. *Limnol. Oceanogr.* **3,** 29-32.
Relates development of this barnacle to temperature and food supply, and discusses duration of the planktonic phase.

Bolster, G. C. (1958). On the shape of herring schools. *J. Cons. Int. Explor. Mer.* **23,** 228-234.
Relation, by echo-sounding, of herring shoals to tidal streams and topographic features of the sea-bed.

Brown, J. B. Gilpin- (1959). The reproduction and larval development of *Nereis fucata* (Savigny). *J. Mar. Biol. Ass. U.K.* **38,** 65-80.
Development to the time of settling of *Nereis fucata* closely resembles that of other nereids. Absence of special commensal adaptations during this period suggests that the habit is only assumed after settlement.

Cole, H. A. (1958). Notes on the biology of the common prawn *Palaemon serratus* (Pennant). *Fish. Invest. Lond.* (2), **22** (5), i-ii, 1-22.
Examination of 12 000 animals taken by handnet, trawl and pot from Anglesey and the Menai Straits revealed little difference between the stocks. Data for spawning, carriage of eggs, growth-rate, sexual dimorphism and length of life are contrasted with data from the French and English Channel coasts and some of the differences accounted for in relation to sea temperatures.

Conover, R. J. (1957). Notes on the seasonal distribution of zooplankton in Southampton Water with special reference to the genus *Acartia*. *Ann. Mag. Nat. Hist.* (12), **10** (109), 63-67.

Glover, R. S. (1957). An ecological survey of the drift-net herring fishery of the north-east coast of Scotland. Pt. II. The planktonic environment of the herring. *Bull. Mar. Ecol.* **5,** 1-43.
Discusses methods of collecting and analysing plankton records and results in terms of distribution of species, seasonal and long-term periods and fluctuations of the fishery.

Hancock, D. A. (1959). The biology and control of the American whelk tingle *Urosalpinx cinerea* (Say) on English oyster beds. *Fish. Invest., Lond.* (2), **22** (10), 1-66.
This muricid gastropod introduced from America probably about 1880 has increased greatly in density but not in range, being still confined to the East Anglian and Thames estuaries. The habits and life history are described. Each tingle eats about forty oyster spat a season. Control is suggested by means of curved tiles at low water springs, under which the adults congregate. Spawn can be removed by dredging.

Naylor, E. (1958). Tidal and diurnal rhythms of locomotory activity in *Carcinus maenas* (L.). *J. Exp. Biol.* **35,** 602-610.
The rhythm is analysed into two components, one of diurnal and the other of tidal frequency with peaks in darkness and at high tide respectively. The joint effect results in a semilunar overall peak of activity.

Pike, R. B. & Le Sueur, R. F. (1958). The shore zonation of some Jersey Cumacea. *Ann. Mag. Nat. Hist.* (13), **1** (8), 515-523.

The distribution and population density of six species of Cumacea were related to the degree of exposure of the habitat and to the arithmetic mean grain size of the sand.

Pike, R. B. & Williamson, D. I. (1959). Observations on the distribution and breeding biology of British hermit crabs and the stone crab (Crustacea: Diogenidae, Paguridae and Lithodidae). *Proc. zool. Soc. Lond.* **132,** 551-567.

Seasonal and geographical distribution in the Clyde sea area including notes on breeding season and growth.

Simpson, A. C. (1958). The lobster fishery of Wales. *Fish. Invest., Lond.* (2), **22** (3), 1-33.

Description of the fishery and its history and comparison with those of Devon and Cornwall and of the north-east English coast, with recommendations for the future.

Simpson, A. C. (1959). The spawning of the plaice (*Pleuronectes platessa*) in the North Sea. *Fish. Invest., Lond.* (2), **22** (7), 1-111.

Extends the classic work of Buchanan-Wollaston, incorporating his observations with new data over periods 1935-39 and 1947-50. Presents contour charts of egg numbers, so delimiting the spawning area in the Southern Bight. Spawning here occurs in winter, the peak being in late January. Total egg production is related to fishing intensities and to the age composition of the spawning population, to its fecundity and age of maturation. Speed and direction of drift of eggs and larvae are followed.

Slinn, D. J. (1958). Phosphate and oxygen in sea-water off Port Erin during 1957. *Rep. Mar. Biol. Sta. Pt. Erin.* No. 70, 27-30.

Graphic presentation of hydrographic data and discussion of significance.

Southward, A. J. (1958). The zonation of plants and animals on rocky sea shores. *Biol. Rev.* **33,** 137-177.

A world-wide survey in which the use of the Stephenson system of classification is advocated. The local effects of particular biological and physical factors are discussed. The causes of sharp zonal boundaries require further investigation.

(*b*) Freshwater

Berg, K., Lumbye, J. & Ockelmann, K. W. (1958). Seasonal and experimental variations of the oxygen consumption of the limpet *Ancylus fluviatilis* (O. F. Müller). *J. Exp. Biol.* **35,** 43-73.

A spring and summer maximum is associated with reproductive activity. The oxygen consumption temperature relationship was shown (with suitable qualifications) to follow Krogh's curve. The regression of oxygen consumption on body weight is also studied.

Brinkhurst, R. O. (1959). The habitats and distribution of British *Gerris* and *Velia* species. *J. Soc. Brit. Ent.* **6,** 37-44.

Notes on habitats and new vice-county records.

Mann, K. H. (1959). On *Trocheta bykowskii* Gedroyć, 1913, a leech new to the British fauna, with notes on the taxonomy and ecology of other Erpobdellidae. *Proc. zool. Soc. Lond.* **132,** 369-379.

T. bykowskii is reported from Windermere and Belfast; its limited European distribution is discussed. Significant habitat factors for other Erpobdellidae appear to be the presence of low oxygen concentrations and occasional drying out of the habitat.

Mučibabič, S. (1956). Some aspects of the growth of single and mixed populations of flagellates and ciliates. The effect of temperature on the growth of *Chilomonas paramecium*. *J. Exp. Biol.* **33,** 627-644.

Populations maintained at a variety of different temperatures showed a rise and fall of growth-rate with temperature but a little change in yield over a wide range. The size of the organisms was least at an intermediate temperature so that this effect modifies the yield relationship. The effects of temperature on shape and on thermal coefficients of growth are discussed.

Reynoldson, T. B. (1958). Triclads and lake typology in northern Britain—qualitative aspects. *Verh. int. Ver. Limnol.* **13,** 320-330.

Analyses the occurrence of triclad Turbellaria in over one hundred lakes in various areas of north Britain, discussing their relations with physico-chemical and other habitat characteristics.

Scott, D. (1958). Ecological studies on the Trichoptera of the River Dean, Cheshire. *Arch. Hydrobiol.* **54,** 340-392.

Quantitative sampling of caddis larvae in relation to microhabitats of the substrate, correlated with measurements of current, oxygen concentration, temperature, over a period of 2 years reveal distinctive species preferences. Larvae which feed mainly on dead organic remains occur at currents below 20 cm/sec, where deposition is active. Alga feeders are on the exposed faces of stones in currents between 20 and 40 cm/sec, while carnivores live mostly below stones in currents of over 40 cm/sec. Positive correlation is shown between density and size of stone. Seasonal changes and flood effects are followed for different species, and pupation sites are discussed.

Toner, E. D. (1959). Predator and prey relationships. *Salm. Trout. Mag.* (156), 104-110.

Discusses relative growth-rates, survival and behaviour of *Esox lucius* and *Salmo trutta.*

Tungate, D. S. (1958). Echo-sounder surveys in the autumn of 1956. *Fish. Invest. Lond.* (2), **22** (2), 1-17.

Contour mapping of herring densities by echo-sounder, tracing of movements of shoals and concentrations of fish, supported by catch data from fishing vessels called by radio communication.

(*c*) Land

Ashby, K. R. (1959). Prevention of regeneration of woodland by field mice (*Apodemus sylvaticus* L.) and voles (*Clethrionomys glareolus* Schreber and *Microtus agrestis* L.). *Quart. J. For.* **53** (3), 228-236.

A major cause of decay of woodlands is excessive numbers of voles and field mice, which eat the seed and seedlings of some common trees. Of seeds put out in tins, all but 114 of 3000 peas disappeared in 2 days, and all but 108 of 1200 sycamore seeds in a fortnight.

Banks, C. J. & Nixon, H. L. (1958). Effects of the ant, *Lasius niger* L., on the feeding and excretion of the bean aphid, *Aphis fabae* Scop. *J. Exp. Biol.* **35,** 703-711.

By labelling plant sap with radio phosphorus it is shown that attendance by ants increases the rate of feeding and excretion of the aphids.

Beven, G. (1959). The feeding sites of birds in dense oakwood. Bookham Common, Survey. *Lond. Nat.* **38** (1958), 64-73.

Observations on over fourteen species in Surrey during 1956-58. More fed in the trees and shrubs than on the ground and herbage. Blue tits (*Parus coeruleus*) showed the greatest preference for the canopy, great tits (*P. major*) for the branches of shrubs, marsh tits (*P. palustris*) for the twigs and leaves of shrubs, and coal tits (*P. ater*) for tree trunks. Blue tits and long-tailed tits (*Aegithalos caudatus*) were dominant in the canopy and shrub layer, except in the breeding season, tree creepers (*Cyrthia familiaris*) and blue tits on the tree trunks, wrens (*Troglodytes troglodytes*) in the herbage, and blackbirds (*Turdus merula*) and robins (*Erithacus rubecula*) on the ground, where the former fed almost exclusively.

Blackith, R. E. (1958). An analysis of polymorphism in social wasps. *Insectes Sociaux,* **5** (3), 263-272.

Morphometric analysis of structural types in *Vespula germanica, V. rufa* and *V. vulgaris* demonstrates sexual dimorphism, polymorphism and caste status in quantitative terms. The whole is related to modes of growth during larval instars.

Blackith, R. E. & Stevenson, J. H. (1958). Autumnal populations of wasps nests. *Insectes Sociaux,* **5** (4), 347-352.

Records excess of males and absence of virgin queens in one nest of *Vespula vulgaris* and large numbers of immature workers in another in autumn 1957; also marked segregation of adult forms. Infestation of virgin queens, but not males and workers, with a mermithid nematode is recorded and discussed.

Bouldin, L. E. (1959). Survey of house martin colonies in east Lancashire. *Brit. Birds*, **52,** 141-149.

486 nests in 122 colonies in an incompletely covered area of 452 000 acres. Most were in suburbs of industrial towns and rural areas. The type of building was not important. Over 80% within 400 yards of a large sheet of water. Colonies mostly of from one to four, maximum thirty-one nests.

Bursell, E. (1955). The transpiration of terrestrial arthropods. *J. Exp. Biol.* **32,** 238-255.

The permeability of the cuticle is shown to be limited by lipoids in a similar manner to that of insects. Owing to shrinkage and closer packing of lipoid molecules, rate of desiccation falls off progressively, as the animal dries out.

Corbet, P. S. (1956). Experimental factors influencing the induction and termination of diapause in the emperor dragonfly, *Anax imperator* Leach (Odonata: Aeshnidae). *J. Exp. Biol.* **33,** 1-14.

Studies on the effect of photoperiod on diapause.

Coulson, J. C. (1959). The plumage and leg colour of the kittiwake and comments on the non-breeding population. *Brit. Birds*, **52,** 189-196.

Non-breeding kittiwakes frequent colonies in large numbers and occupy ledges and even occupied nests in the absence of parents. A proportion, especially of second summer birds, have greenish-yellow markings on legs and feet.

Creed, E. R., Dowdeswell, W. H., Ford, E. B. & McWhirter, K. G. (1959). Evolutionary studies on *Maniola jurtina*: the English mainland, 1956-57. *Heredity*, **13,** 363-391.

The 'reverse of a cline' in spot pattern of the females of the meadow brown butterfly observed at the boundary between the south English and east Cornish populations is described and examined in detail. An explanation is offered on the basis of unspecified strong selective forces operating on characters believed to be genetically linked with spotting.

Crowcroft, P. & Rowe, F. P. (1958). The growth of confined colonies of the wild house-mouse (*Mus musculus* L.): the effect of dispersal on female fecundity. *Proc. Zool. Soc. Lond.* **131,** 357-365.

The proportion of non-fecund females in very dense captive populations is low compared with wild ones. When allowed to spread into larger pens the proportion of fecund females increases.

Edney, E. B. & Spencer, J. O. (1955). Cutaneous respiration in woodlice. *J. Exp. Biol.* **32,** 256-269.

The general integument is shown to be responsible for up to 50% of respiration (the remainder being performed by the pleopods). In dry air the cutaneous respiration is inhibited and this affects longevity at low humidities.

Gibson, J. A. (1958). The 1956 census of gannets (*Sula bassana*) on Ailsa Craig. *Glasgow Bird Bull.* **7,** 7-8.

There was a surprising decrease of over 2000 pairs, to 8063 pairs, since 1955.

Gibson, J. A. (1958). The 1957 census of gannets (*Sula bassana*) on Ailsa Craig. *Glasgow Bird Bull.* **7,** 8-9.

The 1956 decrease continued, numbers falling to 7742 pairs.

Gislén, T. & Kauri, H. (1959). Zoogeography of the Swedish amphibians and reptiles with notes on their growth and ecology. *Acta Vertebratica*, **1** (3), 195-397.

A comprehensive account of the Swedish distribution, with spot maps, of all species of amphibians and reptiles, with notes on their ecology and breeding, and a brief discussion of the past history of the groups in north-east Europe.

Greenaway, R. D. (1958). The Tinkinswood cat. *Trans. Cardiff Nat. Soc.* **85,** 16-20.

Examination of animal and other material from the excavation, about 40 years ago, of a megalithic chambered tomb at Tinkinswood, Glamorgan, affords no support to a recent suggestion by archaeologists that the domestic cat was known in Britain in neolithic times.

Harper, W. G. (1959). Roosting movements of birds and migration departures from roosts as seen by radar. *Ibis*, **101**, 201-208.

Starlings cause the most striking displays. The break-up of flocks leaving roosts on migration flights is more rapid at night than by day.

Harrison, C. J. O. & Forster, J. (1959). Woodlark territories. *Bird Study*, **6**, 60-68.

Describes vegetation and general characteristics of a territory occupied for several years by woodlarks in Surrey, and the movements of the occupants during the season. Comparison is made with another territory elsewhere.

Heath, J. (1959). The autecology of *Eustroma reticulata* Schiff. (Lepidoptera: Geometridae) in the Lake District with notes on its protection. *J. Soc. Brit. Ent.* **6**, 45-51.

Discusses the relation between distribution and population fluctuations and rainfall. *E. reticulata* only feeds on *Impatiens noli-tangere*.

Homes, R. C. (1958). A ten-year review of duck counts in the London area. *Lond. Bird. Rep.* **22** (1957), 36-49.

Includes tables and histograms showing the results of counts of ten duck species regularly present in winter made on some thirty waters during October-March in each of the ten seasons ending 1956-57. The number of hard winters during the period was not unusual. Numbers of mallard, teal, wigeon, pochard and tufted duck increased substantially during the latter half of the period; those of goosander increased slightly, and those of gadwall, goldeneye, smew and shoveler showed no important change. The trends for each are briefly discussed.

Jackson, R. M. (1958). Some aspects of soil fungistasis. *J. Gen. Microbiol.* **19**, 390-401.

Fungistasis was generally shown in English soils but not in very acid raw humus.

Kikkawa, J. (1959). Habitats of the field mouse on Fair Isle in spring 1956. *Glasgow Nat.* **18**, 65-77.

Cover, availability of food and the presence of house mice and rabbits were considered to be the factors responsible for the distribution of the island race *Apodemus sylvaticus fridariensis*.

Krausé, A. G. Carolsfeld- (1959). On the fluctuation of insect populations. *Ent. Rec.* **71**, 1-5.

Observations in Denmark, where, although very small areas with natural biotopes now remained, the insect fauna is richer than in neighbouring countries with large areas of untouched land, indicate that change of climate, not of biotopes, is responsible for the decline in numbers or extinction of many species. Cultivation of the greater part of a heathland area of 2500 sq. km did not influence the number of species on those parts of it left as nature reserves, and a large coherent biotope is considered no more advantageous to a species than one split up into smaller scattered areas. Coniferous woods, which formerly almost completely covered Denmark, were absent between about 2500 B.C. and about A.D. 1730; since their return, only some dozen macrolepidoptera have been added to the fauna. Observations in two woodlands remote from others indicate that at least a century is required for full colonization of isolated areas.

Lack, D. (1959). Watching migration by radar. *Brit. Birds*, **52**, 258-267.

A brief history of bird-detection by radar, descriptions of photographs of bird-echoes, and a review of the ornithological results.

Landa, M. (1959). Climatic fluctuations and their effect on annual growth rings and on growing stock. *Scot. For.* **13**, 154-162, 164.

Useful, non-technical summary with many foreign references. Some zoological notes. Fluctuations are long-term ones. Much Finnish and Scandinavian work on animals is not noted.

Lindahl, K. Curry- (1958). Djurgeografi, populations-dynamik och nutida faunaförändringar. *Ymer*, **1**, 5-57.

A broad discussion of the zoogeography of Sweden and recent faunistic changes viewed against the history of glacial and post-glacial climatic changes in Europe. Relates primarily to vertebrates.

London Natural History Society (1959). The survey of Bookham Common. Seventeenth year. Progress Report. *Lond. Nat.* **38** (1958), 57-63.

Includes a list of Heteroptera and Coleoptera new to the Common, the results of censuses in 1956 and 1958 of singing males of eight woodland bird species and some observed population trends among them, and the results of analyses of tawny owl pellets collected during 1951-54 and 1955-58. Other papers include one by G. Beven on the feeding sites of birds in dense oakwood.

Mere, R. M. (1959). *Nothris congressariella* Bruand on Tresco. *Ent. Rec.* **71,** 35-37.

Observations on the bionomics in Tresco, from which this species was first recorded for the British Isles in 1957. The food-plant there is *Scrophularia scorodonia*, from which it is not recorded in continental Europe, but though this plant was plentiful, the distribution of *Nothris* was limited.

Milne, A. (1959). Biology and ecology of the garden chafer, *Phyllopertha horticola* (L.). 5. The flight season: sex proportions. *Bull. Ent. Res.* **50,** 39-52.

In the English Lake District females begin to emerge 2 to 6 days after the males according to weather, primary emergence being complete in a fortnight. Changes in sex ratio depend on relative dates of emergence and the slightly longer life of the adult female. Sex differences in behaviour are discussed.

Milne, A. (1959). Weather, enemies and natural control of insect populations. *J. Econ. Ent.* **152,** 532-533.

Develops the author's views expressed in 1957, *Canad. Ent.* **89,** 193-213, and criticized by DeBach, P., 1958, *J. Econ. Ent.* **51,** 474-484.

Murton, R. K. (1959). Attacking wood-pigeons in their nests. *Agriculture*, **66,** 199-201.

Nest destruction in late July and mid-September will kill 65% of the young, and destruction in mid-July, late August and mid-October will kill over 80%. Few wood-pigeons arrive in England from abroad.

Peet, W. M. (1959). Starlings affected by smog. *Brit. Birds*, **52,** 238.

The morning after a day of dense fog at Sleaford, Lincolnshire, main thoroughfares were littered with dead starlings which had been injured by impact. A sample showed deaths were due to asphyxia from severe smog.

Robson, R. W. (1959). Flightless condition of common scoter. *Brit. Birds*, **52,** 268.

Instances of common scoters flightless through moult, chiefly in November.

Roots, B. I. (1956). The water relations of earthworms. II. Resistance to desiccation and immersion, and behaviour when submerged and when allowed a choice of environment. *J. Exp. Biol.* **33,** 29-44.

Several species can survive desiccation which reduces water content from about 80% to 20%. They can survive nearly a year submerged in fully aerated water. Eggs can hatch and young feed when immersed. Most species, but not all, avoid waterlogged soil if given the choice; this may explain their surfacing behaviour after rain.

Sage, B. L. (1958). A new gull roost in the London area. *Lond. Bird Rep.* **22** (1957), 50-51.

A new reservoir in south-western Herts., filled during spring and summer of 1955, was used as a gull roost from the winter of the same year, and in consequence the number of gulls roosting in the county, estimated at 5670 in early January 1953, rose to 23 440 in January 1958. This is the only roost in the county used by greater black-backed gulls and by large numbers of herring and common gulls, and the approximate numbers of these and of black-headed gulls using it in January 1958 were 150, 4000, 1850 and 9000 respectively.

Southwick, C. H. (1958). Population characteristics of house mice living in English corn ricks: density relationships. *Proc. Zool. Soc. Lond.* **131,** 163-175.

Demographic data (reproductive and mortality) from very crowded ricks show little evidence of expected differences from non-crowded colonies (fertility is somewhat lower and embryo resorption and fighting between males are higher). The lack of clear differences is attributed to the high quality of food and cover.

Thompson, J. L. Cloudsley- (**1956**). Studies in diurnal rhythms. VII. Humidity responses and nocturnal activity in woodlice (Isopoda). *J. Exp. Biol.* **33,** 576-582.
Four species are shown to be nocturnal in habit in proportion to their inability to tolerate desiccation.

Uffen, R. W. J. (**1959**). On the insect fauna of an area of Thames-side. *Lond. Nat.* **38** (1958), 54-56.
The insect fauna of a strip of waste land bordering the Thames in western London includes a number of species of restricted distribution or recent establishment elsewhere, and many normally associated with the plant species represented were absent. The area provides one of the links between Essex coastal marshes and rubbish tips and open areas in western Middlesex, facilitating the rapid spread of invading European species.

Woodroffe, G. E. (**1959**). Notes on some Hemiptera-Heteroptera from Witley Common, Surrey. *Entomologist,* **92,** 6-13.
Includes information on habitats, food-plants, abundance and distribution for many of the sixty-seven species found, chiefly on grass-heath, though some were in adjoining woodland or scrub. *Globiceps salicicola* is recorded from Sussex for the first time and from Britain for the second.

2. METHODS, APPARATUS, POPULATION STATISTICS AND TAXONOMIC STUDIES OF USE TO ECOLOGISTS

Birkett, L. (**1957**). Flotation technique for sorting grab samples. *J. Cons. Int. Explor. Mer.* **22** (3), 289-292.

Briggs, A. R. Mead- (**1959**). The larva of *Spilopsyllus cuniculi* (Dale) (Siphonaptera). *Proc. R. Ent. Soc. Lond.* (A), **34,** 27-33.
The larva is described and the three instars can be separated on the basis of head width measurements.

Brindle, A. (**1959**). Notes on the larvae of the British Rhagionidae and Stratiomyidae with a key to the genera. *Ent. Rec.* **71,** 126-133.
Notes on the general morphology of larvae of the two families. Habitats are included as characters in the key.

Cameron, J. (**1959**). The larval and post-larval stages of *Gymnammodytes semisquamatus* (Jourdain). *J. Mar. Biol. Ass. U.K.* **38,** 17-25.
Describes development from egg to juvenile of this sand eel, and considers larvae of Ammodytidae in general.

Clinton, E. C. Pelham- (**1959**). *Coleophora sternipennella* (Zetterstedt) (Lep, Coleophoridae) a new British species: with a key to the British *Coleophora* on *Chenopodium* and *Atriplex. Entomologist,* **92,** 120-124.

Edwards, C. A. (**1959**). A revision of the British Symphyla. *Proc. Zool. Soc. Lond.* **132,** 403-439.
In addition to comprehensive keys there are notes on distribution, collecting and mounting techniques.

Heath, J. (**1958**). The British Eriocraniidae and Micropterygidae. *Proc. S. Lond. Ent. nat. Hist. Soc.* **1957,** 115-125.
Includes brief descriptions of the adults and larvae, with seasonal dates, habitats and distribution, for each species, and keys for the separation of the adults.

Jones, J. D. (**1959**). A new tonometric method for the determination of dissolved oxygen and carbon dioxide in small samples. *J. Exp. Biol.* **36,** 177-190.
Presents a method for analysing both gases in samples of less than 1 ml of water and biological fluids which might be adapted for field use but requires about 30 min for each determination. The limitations of other methods are discussed.

Gabbutt, P. D. (1959). The instars of the wood cricket *Nemobius sylvestris* (Bosc) (Orthoptera : Gryllidae). *Proc. R. Ent. Soc. Lond.* (A), **34,** 37-43.
Early instars are separated on the basis of head width measurements but the fifth and later instars can be sexed and separated morphologically (*see* Gabbutt, 1959, *J. Anim. Ecol.* **28,** 15-42).

Hickin, N. E. (1959). Larvae of the British Trichoptera—the Beraeidae. *Proc. R. Ent. Soc. Lond.* (A) **34,** 83-89.
The larvae of *Beraeodes minuta, Beraea maurus, B. pullata* and *Ernodes articularis* are described and figured, and a key is given for their separation.

Kutkuhn, J. H. (1958). Notes on the precision of numerical and volumetric estimates from small-sample concentrates. *Limnol. Oceanogr.* **3,** 69-83.
Comparison of techniques for measurement of littoral plankton populations.

MacDonald, T. H. (1959). Identification of ammocoetes of British lampreys. *Glasgow Nat.* **18,** 91-95.
A useful key.

Mayr, E. (1959). Trends in avian systematics. *Ibis,* **101,** 293-301.
Population and phylogenetic systematics are areas of avian systematics favourable for active expansion.

Milne, A. (1959). The centric systematic area-sample treated as a random sample. *Biometrics,* **15,** 270-297.
Analyses statistically and by consideration of natural samples the problem of whether or no centric systematic samples can be treated as if random, and concludes that, used intelligently, they may be.

Morton, J. E. & Machin, J. (1959). A key to the land snails of the Flatford area, Suffolk. *Field Studies,* **1,** 57-71.
Keys, with very clear illustrations of critical features, to a large proportion of the British land snails. Some notes on local ecology.

Schultz, V. & Muncy, R. J. (1957). An analysis of variance applicable to transect population data. *J. Wildlife Mgmt.* **21,** 274-278.
Statistical analysis applied to various types of line transect observations.

Woodroffe, G. E. (1959). Two forms of *Coranus subapterus* Degeer (Hem. Reduviidae) associated with distinct habitats. *Entomologist,* **92,** 125-128.
Specimens from heather heath and from sand dunes showed fairly constant morphological differences. A key for their separation is included.

3. PARASITES

Clinton, E. C. Pelham- (1959). Parasites of *Nothris congressariella* Bruand. *Ent. Rec.* **71,** 88.
Horogenes sp., *Gelis instabilis* and *Apanteles sicarius* were bred from larvae collected in Tresco during August 1958.

Gibson, T. E. (1959). Nematodiriasis in sheep. *Agriculture,* **66,** 126-129.
Pathogenic infestations of young lambs by *Nematodirus* sp. can be avoided if, for the first 8-10 weeks, lambs are grazed only on land which did not carry lambs the previous year, or treated by drugs.

Mason, J. (1958). The occurrence of *Nicothoë astaci* Audouin & Milne Edwards on Scottish lobsters. *Mar. Res.,* No. 9, 1-8.
Estimates of infestation rates on *Homarus vulgaris* in relation to size of host, with a discussion of the effects on the lobsters.

Mason, J. (1959). The biology of *Nicothoë astaci* Audouin & Milne Edwards. *J. Mar. Biol. Ass. U.K.* **38,** 3-16.

Describes the adult male and female, breeding, life cycle and growth and the relations between the parasite and the moulting of its lobster host.

Perkins, J. F. (1959). *Idiogramma* Foerster, a genus previously unrecorded from the British Isles (Hymenoptera, Ichneumonidae). *Entomologist,* **92,** 197.

I. euryops parasitizing *Xyela julii* in north Sutherland.

Ring, M. (1959). Studies on the parasitic Protozoa of wild mice from Berkshire with a description of a new species of *Trichomonas*. *Proc. Zool. Soc. Lond.* **132,** 381-401.

Primarily a taxonomic study. Contains a comparison with Elton's Bagley Wood, Berkshire, lists of mouse parasites: there is little similarity.

Rowlands, W. T. (1959). Liver fluke in Wales. *Agriculture,* **66,** 170-173.

Good grazing management, especially drainage, use of molluscicides and routine dosing can reduce fluke infestation in sheep and cattle.

Thomas, J. D. (1958). Studies on the structure, life-history and ecology of the trematode *Phyllodistomum simile* Nybelin 1926 (Gorgoderidae: Gorgoderinae) from the urinary bladder of brown trout, *Salmo trutta* L. *Proc. Zool. Soc. Lond.* **130,** 397-435.

Although quite widely spread among different host species in other areas, the parasite was confined to trout in the River Teify, where it was more abundant in older fish. The intermediate host is *Sphaerium corneum.*

Waterston, G. (1959). Golden eagle with tuberculosis and aspergillosis. *Brit. Birds,* **52,** 197-198.

A golden eagle in good condition found dead in an eyrie in late April had advanced and generalized tuberculosis and aspergillosis.

4. FOOD AND FOOD HABITS

Drinnan, R. E. (1958). The winter feeding of the oystercatcher (*Haematopus ostralegus*) on the edible mussel (*Mytilus edulis*) in the Conway estuary, North Wales. *Fish. Invest. Lond.* (2), **22** (4), 1-15.

The birds feed on mussels whenever they are exposed by tides both day and night. Each bird eats about its own weight of wet shellfish daily, and, at Morfa, the larger size groups of mussels are removed steadily throughout the winter. Comparisons are made with similar studies elsewhere and differences discussed.

Lasker, R. & Giese, A. C. (1956). Cellulose digestion by the silverfish, *Ctenolepisma lineata. J. Exp. Biol.* **33,** 542-553.

Silverfish can digest cellulose with the same efficiency as a cow and can gain weight, but cellulose does not suffice as a complete diet. This ability does not depend on the presence of bacteria in the gut and the animal produces its own cellulose.

Poole, T. B. (1959). Studies on the food of Collembola in a Douglas fir plantation. *Proc. Zool. Soc. Lond.* **132,** 71-82.

Gut contents of larger species (*Isotoma, Lepidocyrtus, Tomocerus* and *Isotomurus*) were mainly fungus mycelium, some of which was isolated in a viable state (author suggests that the animal therefore disperses the fungi). Smaller species feed on 'humus'.

Tyler, M. J. (1958). On the diet and feeding habits of the edible frog (*Rana esculenta* Linnaeus). *Proc. Zool. Soc. Lond.* **131,** 583-595.

Stomach contents included many flower heads but the species is not very selective. Adults show cannibalistic tendencies.

5. MIGRATION, INTRODUCTIONS AND LOCAL DISTRIBUTION

Allen, A. A. (1959). The Coleoptera of a suburban garden. 6—Brachelytra (Part I). *Ent. Rec.* **71,** 16-20, 39-44.

Notes on the habitat and abundance of a further ninety-eight species. (See 1956, *Ent. Rec.* **68,** 215-222 and abstract in 1958, *J. Anim. Ecol.* **27,** 421.)

Barrett, J. H. (1959). The birds of the parish of Dale, including Skokholm. *Field Studies*, **1**, 1-16.
An annotated list of the birds of this region of Pembrokeshire.

Bassindale, R. & Barrett, J. H. (1957). The Dale Fort marine fauna. *Proc. Bristol Nat. Soc.* **29** (3), 227-328.
A systematic list of the littoral fauna of this Pembrokeshire coast.

Baynes, E. S. A. (1959). Report on migrant insects in Ireland for 1958. *Irish Nat. J.* **13**, 25-29.
Records of Lepidoptera only were received.

Burton, J. F. (1959). Notes on Orthoptera for 1958 from Breconshire, Kent and Oxfordshire. *Ent. Rec.* **71**, 76-77.
Records for some seven species. Many individuals of *Chorthippus brunneus* in very sooty grass at two places in Kent were grey, dark or even almost completely black in colour.

Clinton, E. C. Pelham- (1959). Microlepidoptera new to Scotland. *Ent. Rec.* **71**, 68-72.
Localities, dates and food-plants for fourteen species and one subspecies believed to be new to Scotland.

Cornwallis, R. K. (1959). An immigration of winter visitors. *Bird Study*, **6**, 68-72.
Describes a localized immigration of Turdidae principally directed at Spurn Head and Gibraltar Point in November, and analyses it from ringing recoveries and correlative observations coupled with weather conditions.

Davidson, W. F. (1959). *Phymatodes testaceus* Linn. (Col.) in Cumberland. *Ent. Rec.* **71**, 56.
A new county record.

Davidson, W. F. (1959). Some insects (mainly Coleoptera) of the Caldbeck Fells in Cumberland. *Ent. Rec.* **71**, 83-86. Addendum. *T.c.*, 115. Addenda to the Coleoptera of the Caldbeck Fells. *T.c.*, 140.
A list of some 120 beetles, with an additional eighteen in the addenda, an Empid, a bumblebee and several moths from the Caldbeck Fells (including Skiddaw and Saddleback) collected over a period of 2 years. Large numbers of *Geotrupes vernalis*, one of the most abundant species, were eaten by foxes, and droppings composed almost entirely of the elytra were observed.

Davidson, W. F. (1959). *Limosina racovitzai* Bezzi (Dipt.) in Cumberland. *Ent. Rec.* **71**, 115.
L. racovitzai var. *macrops* was taken in moles' nests in late November 1958. A first record for the county.

Delany, M. J. (1958). The mammal fauna of the Clyde area. *Glasgow Nat.* **18**, 15-27.
A faunistic list with detailed records by vice-county.

Edwards, C. (1959). Occurrence of the chondrophore *Velella velella* (L.) on western Scottish coasts. *Glasgow Nat.* **18**, 78-81.
A review of recent and earlier records.

Fairclough, R. (1959). *Depressaria prostratella* Constant: a first record in Britain. *Ent. Rec.* **71**, 27-28.
Taken at mercury-vapour light, Ashdown Forest, 31 August 1957.

Gibson, J. A. (1957). The waders of Balgray and Waulkmill Glen dams, east Renfrewshire. *Glasgow Bird Bull.* **6**, 22-28.
Notes covering a period of over 60 years.

Gifford, D. (1959). Notes on Scottish woodland insects: 1. The small ermine moth, *Yponomeuta evonymella* (L.) (Lepidoptera: Yponomeutidae). *Scot. For.* **13**, 142-143.
Infests *Prunus padus*. High numbers in 1959 as far north as Perthshire.

Goodacre, M. J. (1959). The origin of winter visitors to the British Isles. *Bird Study*, **6**, 37-50.

The first of a series of analyses of BTO ringing returns and recoveries; deals with the blackbird, the British wintering population of which comes from north-east Europe. Analyses of movements are made.

Groves, E. W. (1959). Some entomological records from the Cripplegate bombed sites, City of London. *Lond. Nat.* **38** (1958), 25-29.

Includes lists, with dates and, in some cases, habitats, for species of Coleoptera, Hemiptera, Hymenoptera, Neuroptera, Orthoptera, Dermaptera and other arthropods, with a brief discussion of the climate of the area, the source of the insect fauna, and factors affecting its establishment.

Harrison, J. W. Heslop- (1959). An additional inland locality for the brown argus, *Aricia agestis*, in Co. Durham. *Entomologist*, **92**, 188.

Hickling, G. (1959). The grey seals of the Farne Islands. *Oryx*, **5**, 6-11.

A brief account of the history of the grey seal colony on the Farne Islands with recent counts of its numbers and of tagging experiments by the Northumberland and Durham Natural History Society, also comments on the recent experimental thinning of the number of calves. It is followed by a reprint (pp. 11-15) of an article by E. A. R. Ennion entitled 'Should the seals be killed?'

Hunt, J. M. Chalmers (1959). *Eupithecia valerianata* Hüb. in Kent. *Ent. Rec.* **71**, 55.

Larvae on *Valeriana officinalis* collected in July and August 1958 constitute the first record for this county.

Hunter, W. R. (1958). New and newly confirmed distribution records of non-marine molluscs in the west of Scotland (IVth paper). *Glasgow Nat.* **18**, 37-44.

Eighteen species listed.

Hunter, W. R., Slack, H. D. & Hunter, M. R. (1959). The lower vertebrates of the Loch Lomond district. *Glasgow Nat.* **18**, 84-90.

A systematic list of reptiles, Amphibia and freshwater and marine fish.

Lack, D. (1959). Migration across the North Sea studied by radar. Part 1. Survey through the year. *Ibis*, **101**, 209-234.

Three years' observations disclose a huge eastward movement from Norfolk in spring, arrivals from north-west presumed to be directly from Scandinavia in late autumn, and presumed redirected eastward movements of drifted arrivals, movements not recorded on visual evidence.

Lack, D. & Williamson, K. (1959). Bird-migration terms. *Ibis*, **101**, 255-256.

Definitions agreed at a conference held in January 1959 at the Edward Grey Institute, Oxford.

Lampel, G. P. (1959). Additions to the county records of spiders with notes on two species of interest. *J. Soc. Brit. Ent.* **6**, 52-54.

Two species new to Britain, including *Tegenaria pagana*, a Canary Islands species, established in banana warehouses. New county records.

Lees, F. H. (1959). *Plusia biloba* Steph. in Devon. *Ent. Rec.* **71**, 28.

Previously recorded in Britain only from Cardigan.

McMillan, N. F. (1958). The molluscan fauna of Storeton Woods, Wirral, Cheshire. *Proc. Liverpool Nat. Fld. Cl.* **1957**, 26-27.

Thirteen species recorded from a strip of pine-birch woodland with much bracken, on acid soil.

Massee, A. M. (1959). The Hemiptera-Heteroptera of Kent (Supplement I). *J. Soc. Brit. Ent.* **6**, 55-56.

Adds nineteen species and two varieties to Massee, A. M. (1954). *Trans. Soc. Brit. Ent.* **11**, 245-280.

O J.A.E.

Matheson, C. (1958). The black rat at British seaports. *Pest Technology*, **1**, 4-7.
Comparison with a survey published by the author in 1939, *J. Anim. Ecol.* **8**, 76-93, indicates that in most ports the black rat has greatly decreased in numbers.

Niblett, M. (1959). The gall mites (Eriophyidae) of the London area. *Lond. Nat.* **38** (1958), 51-54.
A list, with localities and food-plants, of species found within a 20-mile radius of St Paul's Cathedral.

Parmenter, L. (1959). A morning in Pembrokeshire collecting Diptera. *Ent. Rec.* **71**, 99-100.
Some sixty species are listed, with habitats.

Parmenter, L. (1959). The Diptera about Dale Fort Field Centre, Pembrokeshire. *Ent. Rec.* **71**, 133-135, 157-160, 191-196.
Two hundred and fifty-five species collected in August 1948 are listed under the various habitats, which are described, and which include beaches, a bracken area, woodland, hedgerows, estuarine habitats, cliff tops, windows and flowers. One hundred and eighteen species were found on flowers of twenty-three species.

Paul, A. R. (1958). Eastbourne marine shore fauna. Being notes on the distribution of species occurring in the neighbourhood of the Beachy Head and Holywell areas of Eastbourne. *Proc. Zool Soc. Lond.* **131**, 527-557.
Notes on collecting grounds and distribution followed by a systematic fauna list.

Richter, R. (1959). The present distribution of *Potamopyrgus jenkinsi* (Smith) in Buchan and the southern Moray Firth area. *Glasgow Nat.* **18**, 98-105.
A detailed survey by vice-counties of an operculate snail which is widely dispersed within 6 miles of the coast. It is present in all brackish estuaries and salt marshes, but absent from markedly acid water.

Roe, K. M. (1958). The littoral harpacticids of the Dalkey (Co. Dublin) area with descriptions of six new species. *Proc. Roy. Irish Acad.* **59** B, 221-255.
Lists 106 species of harpacticid copepods obtained by washing algae and stones and by netting pools, with short ecological notes. Includes descriptions of six out of eight new species and four hitherto unknown males.

Russell, F. S. (1959). Some observations on the scyphomedusa *Atolla*. *J. Mar. Biol. Ass. U.K.* **38**, 33-40.
Records *A. parva* and *A. wyvillei* as permanently present in the Bay of Biscay.

Ruttledge, R. F. (1959). The crossbill invasion in Ireland in 1958. *Irish Nat. J.* **13**, 33-36.
Records from fourteen counties, with some notes on feeding habits.

Salmon, H. M. (1959). Ornithological notes 1956-57. *Trans. Cardiff Nat. Soc.* **86**, 19-21.
Notes on fifty-two of the more unusual and interesting species seen in Glamorgan and Monmouthshire from October 1956 to September 1957. They include three species new to Glamorgan—little egret, Sabine's gull and little bunting.

Seago, J. H. (1959). Butterflies of south Yorkshire and adjacent areas including notes on their changes in distribution during the last century. *Ent. Rec.* **71**, 5-10.
An annotated list and a short discussion of the changes noted. Some species that have become extinct have done so in many other areas in Britain, whereas others have been affected only in neighbouring districts. Industrialization and drainage or cultivation have provided artificial habitats that have been colonized by several species.

Spooner, G. M. (1959). The occurrence of *Microcharon* in the Plymouth offshore bottom fauna, with description of a new species. *J. Mar. Biol. Ass. U.K.* **38**, 57-63.
Describes *Microcharon harrisi* sp. nov., an isopod from Eddystone shell gravel, and discusses its faunistic and systematic relationships.

Stroyan, H. L. G. (1959). Aphids in Wales. *Nature in Wales*, **5**, 781-784.
Lists of Welsh aphids published up to 1954 comprised almost 200 species. Additional species recorded since that time are listed, and likely habitats for other species discussed from the ecological standpoint.

Venables, L. S. V. & Venables, U. M. (1959). Increase in a Shetland fulmar population. *Brit. Birds*, **52**, 197.
Counts of occupied sites in part of the Fitful Head fulmar colony during the first half of June in 1948, 1949 and 1958 showed averages of 310, 330 and 412 respectively.

Veysey, C. M. (1958). Ham Island Sewage Farm: some further notes on the bird life. *Middle-Thames Nat.* No. 10 (1957), 3-7.
Records for waders, duck, geese, gulls and tern in 1952-56. (See 1953, *Middle Thames Nat.* no. 5, 5-9 and abstract in 1954, *J. Anim. Ecol.* **23**, 206.)

Walls, F. D. E. & Thomas, H. T. (1958). Notes on the birds of the Burnt Islands and some Loch Fyne islands. *Glasgow Bird Bull.* **7**, 9-12.
Status of breeding birds on marine islands in the Kyles of Bute and Loch Fyne.

Warwick, T. (1959). The isopods *Asellus aquaticus* and *A. meridianus* in Scotland. *Glasgow Nat.* **18**, 96-97.
A survey of records by vice-counties. So far the two species have not been found together in Scotland.

Warwick, T. (1959). *Crangonyx pseudogracilis* Bousfield, an introduced freshwater amphipod, new to Scotland. *Glasgow Nat.* **18**, 109-110.
First recorded from England in 1937, the species has now been reported at Grangemouth on the Forth.

Went, A. E. J. (1959). Rare fishes taken in Irish waters in 1958. *Irish Nat. J.* **13**, 31-33.
A new annual report; records of nine species.

Woodroffe, G. E. (1959). *Globiceps salicicola* Reuter (Hem., Miridae) new to Britain. *Entomologist*, **92**, 61-64.
This Mirid was recorded from sandy heathland in Surrey in June 1956. The paper includes a key to the three species of *Globiceps* known in Britain.

de Worms, C. G. M. (1959). A supplement to the butterflies and moths of London and its surroundings. Part 1. *Lond. Nat.* **38** (1958), 33-50.
The records, based on recent collections and the early literature, in this part are supplementary to two earlier lists (*cf.* 1950, *Lond. Nat.* **29**, 46-80, abstract 1951, *J. Anim. Ecol.* **20**, 154 and 1954, *Lond. Nat.* **33**, 101-146, abstract 1955, *J. Anim. Ecol.* **24**, 215) and include a number of new county records.

6. BEHAVIOUR

Baerends, G. P. (1959). The ethological analysis of incubation behaviour. *Ibis*, **101**, 357-368.
A survey of behaviour mechanisms in birds, based mainly on study of the herring gull, which help to secure conditions necessary for the development of eggs during incubation.

Benson, G. B. G. (1959). Display flight of bitterns. *Brit. Birds*, **52**, 267-268.
Three birds rose and circled at 600 or 700 ft up. One bird repeatedly flew immediately above another, and appeared to attempt to rest on its back. One also would fly behind another and strike with the bill at its tail.

Blackith, R. E. (1958). Visual sensitivity and foraging in social wasps. *Insectes Sociaux*, **5** (2), 159-169.
Analyses foraging activities of *Vespula germanica, V. rufa, V. vulgaris* and *Vespa crabro* in relation to the physical environment. Concludes that illumination is the most critical factor, the thresholds being related to the length of the compound eyes, but also being related stochastically to the number of workers foraging.

Boase, H. (1959). Notes on the display, nesting, and moult of the mute swan. *Brit. Birds*, **52,** 114-123.

Displays used in pair-formation are described. Immature birds display, and third-summer birds may normally form pairs in late summer. Family parties keep together till the end of the year. Broods varied from one to eight, most were of four or five.

Dixon, T. J. (1959). Studies on oviposition behaviour of Syrphidae (Diptera). *Trans. R. Ent. Soc. Lond.* **111,** 57-80.

Gives details of the relationship between the numbers of aphids and Syrphidae on broom (*Sarothamnus scoparius*) and the stimuli inducing oviposition responses in *Syrphus luniger* and *Pipizella varipes*. Concludes that syrphids tend to oviposit on broom bushes heavily infected by aphids, eggs are laid close to the aphids, oviposition occurs most frequently with larger aphid colonies and the olfactory stimuli provided by the aphids elicit alighting and oviposition responses in gravid females of *Syrphus luniger*.

Fry, C. H. (1959). Frightened common scoters diving from the wing. *Brit. Birds*, **52,** 197.

Some birds of a flock flying close to the sea surface below an aeroplane scattered but most dived from the wing.

Harthan, A. J. (1959). Hen blackbird killing young. *Brit. Birds*, **52,** 165.

Killed three after carrying them from the nest, the fourth in the nest.

Hinde, R. A. (1957). Behaviour and speciation in birds and lower vertebrates. *Biol. Rev.* **34,** 85-128.

Mainly concerned with the evolutionary aspects of divergence between species. Ecological aspects include habitat selection and factors influencing competition between closely related species.

Hinde, R. A. (1959). Motivation. *Ibis*, **101,** 353-357.

Unitary drive concepts are used to explain certain characteristics of behaviour. Though their value has been proved, the evidence suggests that they have limitations.

Hitchcock, R. E. (1959). Early breeding of crossbill. *Brit. Birds*, **52,** 166.

A juvenile judged to have flown a week earlier seen in the Suffolk Breckland on 1 February 1959.

Laurence, B. R. (1959). Swarming in six species of Empididae (Diptera). *Ent. Rec.* **71,** 37-39.

Observations on swarms of males carrying prey in *Rhamphomyia atra* and *Empis nuntia* and also on swarms of males without prey in *Hilara flavipes* and *Microphorus crassipes* and swarms consisting chiefly of females in *Hilara nigrina* and *H. angustifrons*.

Owen, D. F. (1959). The breeding season and clutch-size of the rook. *Ibis*, **101,** 235-239.

Variations in the breeding season over 6 years near Oxford were correlated with mean air temperatures prior to egg-laying. The number of young raised was greater on average from broods of five than four, but in no instance were all five reared.

Rook, D. A. (1959). Notes on the behaviour of hedgehogs in a suburban garden. *Lond. Nat.* **38** (1958), 30-32.

Includes accounts of three instances of apparently little-known courtship behaviour, in which two animals revolved round each other, either nose-to-nose or at right angles, while the retreating animal made a loud snuffling noise, and which in one case ultimately involved five individuals.

Simmons, K. E. L. (1959). Anting movements and their relation to certain other behaviour patterns. *Ibis*, **101,** 368-372.

Describes anting movements of nine passerine species studied in captivity and in the wild. Anting seems to be a feather maintenance activity, but the exact function of anointing with formic acid has not been discovered.

Thorpe, W. H. (1959). Learning. *Ibis*, **101,** 337-353.

The evaluation of recent studies in the learning abilities of birds.

Tinbergen, N. (1959). Behaviour, systematics, and natural selection. *Ibis*, **101**, 318-330.
The use of behaviour characters in systematics requires true differences and immediate environmental affects to be distinguished cautiously. It is concluded that behaviour characters have not been more subject to selection than other characters.

Trelfa, G. (1959). Early nesting of reed warbler. *Brit. Birds*, **52**, 165-166.
Eggs in a nest at Marbury Mere, Cheshire, were hatching on 19 May 1958.

Venables, U. M. & Venables, L. S. V. (1959). Vernal coition of the seal *Phoca vitulina* in Shetland. *Proc. Zool. Soc. Lond.* **132**, 665-669.
This phenomenon is described, but is relatively unimportant.

Raynsford, L. J. (1959). Early roding of woodcock. *Brit. Birds*, **52**, 268.
A nest in Surrey had hatched out before 30 March 1957. Roding had commenced in two woodlands by 15 (but not 9) February 1958.

Wootton, A. G. (1959). Unusual site of goldcrest's nest. *Brit. Birds*, **52**, 133.
A nest in the hollow stub of a branch 25 ft up, in an oakwood without conifers or ivy clad trees.

7. REPORTS OF ORGANIZATIONS

Cambridge Bird Club (1958). 31st Annual Report, 1957. 24 pp.
Mainly faunistic notes, but deals also with migration and duck counts on the Ouse washes.

Cambridge Bird Club (1959). 32nd Annual Report, 1958. 32 pp.
Includes the usual list of birds seen in Cambridgeshire during the year, with notes on migration in the Wash and elsewhere; duck counts in the Ouse washes; waders seen at Wisbech sewage farm; bird ringing; and movements of herons in the first 2 years after ringing.

Cornwall Bird-watching and Preservation Society (1959). 28th Annual Report, 1958, 76 pp.
Includes the usual classified notes on birds seen in Cornwall and the Scilly Isles during the year, with dates of the arrival and departure of migrants, and a paper on visible migration from the north coast of west Cornwall in autumn.

Devon Bird-watching and Preservation Society (1958). 30th Report, 1957. 84 pp.
In addition to the usual faunistic notes, special reports on the occurrence of the black redstart, the breeding of the spotted flycatcher, the distribution of the cirl bunting, woodlark and common redstart, wildfowl counts and the Spreacombe sanctuary.

Devon Bird-watching and Preservation Society (1959). 31st Report, 1958. 84 pp.
In addition to the usual classified list of birds seen in the county, includes final reports on the black redstart and spotted flycatcher inquiries, and annual reports on wildfowl counts, the cirl bunting and woodlark distribution survey and the redstart distribution inquiry.

Essex Bird Watching and Preservation Society (1958). The Essex Bird Report, 1957. 72 pp. (G. A. Pyman, 99 Galleywood Road, Chelmsford, 4*s*.)
In addition to the usual faunistic notes, reports from the four Essex bird observatories and ringing stations, and results of wildfowl counts.

Essex Bird Watching and Preservation Society (1959). The Essex Bird Report. 1958. 72 pp.
In addition to the classified list of birds seen in Essex during 1958, there are reports on Bradwell Bird Observatory and Romford Ringing Station, and a special report on wildfowl counts in extra-metropolitan Essex.

Lancashire and Cheshire Fauna Committee (1959). Ornithological Report, Part I, 1950-56: Lancashire. 67 pp.
Consists entirely of a classified list of birds occurring in Lancashire during the 7-year period. compiled by C. Oakes.

Middle-Thames Naturalist, No. 10 (1957), 1958.

In addition to annual reports on local ornithology and bird-ringing activities, includes notes on the status of deer in the Chilterns by S. Cowdy and on starling roosts in Windsor Forest by I. M. Walker, and records of waders, duck, geese, gulls and tern at a Berkshire sewage farm in 1952-56 by C. M. Veysey. (See 1953, *Middle-Thames Nat.* no. 5, 5-9 and abstract in 1954, *J. Anim. Ecol.* **23,** 206.)

Oundle School Natural History Society (1959). Report for 1958. 55 pp., duplicated.

Includes reports on the status of wildfowl at the Oundle gravel pits, population studies on tadpoles, and distribution of swan mussels in the River Nene.

BRITISH ECOLOGICAL SOCIETY

SPRING MEETING AT BANGOR (N. WALES)

11-14 April 1958

The meeting opened on the evening of 11 April with a soirée in the Department of Botany. An unusually large and interesting range of exhibits were on display from the Departments of Botany and Zoology and the Nature Conservancy.

At the start of the next morning's session the Hon. Treasurer presented the Society's accounts for 1957. Dr Whitehead explained some of the features of the income and expenditure and the accounts were then formally approved. The rest of the morning was devoted to a series of papers on Land Use. Professor L. Dudley Stamp opened the session with a paper on the mapping of land use. He described the purposes of land-use mapping first as a record on maps of the actual and existing land use. Secondly, an attempt can be made to disentangle the pattern found and explain its underlying physical or historical causes. Professor Stamp then explained the plans for developing land-use surveys on an international basis and illustrated some of the interesting facets by reference to his own pioneer survey in Britain and later surveys in Japan, Cyprus and African territories.

Mr J. A. Taylor followed with a paper entitled 'Growing season; its measurement and mapping'. Mr Taylor first discussed existing data on temperature in relation to growth, in which a variety of methods of measurement have been used. Daily maximum temperatures at or near the ground are better indicators of growth potential than monthly mean Stevenson screen temperatures. In the British Isles growing season is rapidly retarded and reduced by both altitude and distance from the sea, but local factors such as slope, aspect and soil temperature modify these relationships. On a hill near Aberystwyth experimental investigation revealed that growth potential was related to aspect thus: north facing slope 100, east 107, south 148, west 123. Another investigation in south-west Lancashire revealed that peat land is a month later in March-April than adjacent sandland, but by June-July accelerated growth on the peatland as fully compensated for the late start.

Professor R. Alun Roberts then gave a paper on 'Human Settlement and land use in Snowdonia against the background of vegetation ecology in the area', which has been published in full in *J. Ecol.*, **47** (1959), 317-23.

The final paper in the morning was given by Dr R. E. Hughes on 'The ecological approach to problems of land use in Snowdonia', and was based on data from his published account in *J. Ecol.*, **46** (1958), 169-90. Dr Hughes emphasized the effects of climate, soil and vegetation on the numbers of sheep that can be grazed, the importance of the areas of basic drift in the sheep walks, and the probable significance of copper and cobalt. In discussing the improvement of land use a mosaic of forest and grazing with adequate fencing, accessibility and shelter woods was suggested.

A lively discussion followed these four papers in which, as well as the speakers, Professor Burges, Dr Woodhead, Dr Reynoldson, Dr Gorham, Mr Le Cren and Professor Pearsall took part.

In the afternoon the meeting split into two parties. One, consisting mainly of the zoologists, visited the Marine Station at Menai Bridge. Here they were welcomed by Dr Crisp and then embarked on R.V. *Nautilus* for a trip round Puffin Island. On return the laboratory and a series of exhibits were inspected. The other, mainly botanical, party visited Pabo, where Mr D. F. Ball explained the somewhat complex relationships of the local soils, and Little Orme Head, where the vegetation of the limestone cliffs was examined.

Sunday, 13 April, was devoted to excursions; again a choice of two was provided. A larger party went by bus to the Newborough Warren and Llanddwyn Nature Reserves where the extensive and impressive dune formations were inspected. Of particular

interest were the part played by *Salix repens* in dune formation and the extensive and varied slack communities.

The other smaller party were taken in cars (led by Dr Hughes in a fast and intrepid Land Rover) on a tour of sheep walks. The tour started on the drier low altitudes at the northern end of the Conway Valley and ended on the higher and wetter slopes of Snowdon itself to the south of the region; the areas near Llyn Eigiau and Llyn Llydaw were inspected in greater detail. The excursion was memorable for the fascination of the historical detail of land use demonstrated on the sites by Dr Hughes, by the magnificent weather and scenery and by *Saxifraga oppositifolia* in full bloom.

In the evening two series of colour slides were shown in the Botany Department. Dr L. H. Milliner illustrated several features of the vegetation and flora of New Zealand and Professor Richards showed aspects of the vegetation of Ceylon and Siam, especially the forests, and included some excellent photographs of the ruins of Ankowat.

The final session of the meeting on the morning of Monday, 14 April, was held in the Department of Agricultural Botany and was devoted to a second series of papers on Land Use; with reference particularly to areas outside Wales. Professor Pearsall opened the session with a paper entitled 'Land use and soil deterioration in Britain'. Three ideas of interest in relating observed facts to problems of land use are: (*a*) the idea of a relatively stable climax vegetation, which when disturbed goes back to an earlier less productive phase of succcession, (*b*) the idea that vegetation or eco-systems are dynamic and it is necessary to know how land use will affect them, and (*c*) there is evidence in Highland Britain of a trend of change which can be called a new cycle of erosion. Erosion trends can be examined by looking at the accumulations of the products of erosion in lake deposits. Such deposits from the southern Lake District have given evidence that there were two periods of forest clearance through human activity, associated with successive and increasing intensity of soil erosion. There is also evidence of diminution of nitrogen, increased leaching of bases, soil acidification and a change in the calcium-iron ratios of the sediments.

Mr J. M. B. Brown followed with a discussion of 'Ecological considerations in the use of waste land for afforestation'. Waste land can be grouped into four main types: (*a*) lowland, e.g. *Calluna* heaths, (*b*) upland heaths and blanket bogs, (*c*) waste mineral workings and (*d*) coastal sand dunes. In the upland areas climate appears to be the most important factor controlling tree growth and many tree species are tolerant of a range of soils, but in the lowlands where climate is less important soil types affect afforestation. Temperature is particularly important in hill lands. With an increase in altitude there is less seasonal variation in temperature but although the mean winter temperatures may be moderate extremes are low and late frosts are frequent.

A mid-morning break for coffee was combined with an examination of a further series of some twelve exhibits of greenhouse experiments in progress on the roof.

The two final papers were devoted to land use and conservation in Scotland. Dr McVean presented the 'Position and prospects in Scotland' and Dr Lockie followed with a brief review of land utilization in relation to wild birds and mammals. Dr McVean discussed the relations between agriculture, forestry and nature conservation, and the lack, among even the educated public, of a real understanding of the ecological principles of land use. Some estates were experimenting successfully with mixtures of farming, forestry and deer conservation but it would take a long time to restore the fertility of much marginal land and even to demonstrate against prejudice that it could be done. Dr Lockie discussed the effects of the simplification of the habitat by man and the resultant encouragement of pests such as voles, hares and eagles. He thus advocated the diversification of land use and the proper integration of agriculture, forestry and wild life conservation.

These papers were followed by a discussion that ranged over a number of topics and in which Professor Burges, Professor Pearsall, Dr Hughes, Dr Conway and Dr Gorham took part. The meeting ended when the President thanked our hosts for an unusually enjoyable and stimulating meeting. We are indebted to Professor Richards and Professor Alun Roberts for the hospitality of their Departments, to Mr Greig-Smith who made many of the arrangements, to Dr R. E. Hughes and the Nature Conservancy, to

Dr Crisp, and finally to the Warden of the University Hall for excellent accommodation. We left Bangor with the impression that it must be one of the most active centres of pure and applied ecological research in the country.

E. D. Le Cren

SUMMER MEETING AT FLATFORD MILL

10-15 July 1958

The Summer Meeting for 1958 was held from 10-15 July at the Flatford Mill Field Centre of the Field Studies Council. A disappointingly small number of about fifteen members assembled on 10 July, and immediately found themselves in a habitat dominated by John Constable and the hospitality of Mr and Mrs Bingley and the Centre staff. In the evening a soirée was held in the fourteenth-century hall of Mr Bingley's house, when he gave an illustrated talk on the district and some of the areas to be visited.

On the morning of 11 July, we visited Dodnash Wood. This consists mostly of the remains of oak standards with sweet-chestnut coppice and in one area coppiced elm. One of the valleys with a London clay bottom and two medieval fish ponds were examined with a flora dominated by elder and solid stands of *Urtica dioica*. The afternoon was spent on the River Stour in boats, inspecting the aquatic vegetation and freshwater fauna upstream to Dedham Mill Pool. Here, elvers were seen migrating up through the sluices and opportunity was taken to inspect the architecture of the old market town.

Saturday, 12 July, was devoted to the fens in the Waveney-Little Ouse valley, under the guidance of Dr Francis Rose. Redgrave Fen was visited first, where the striking spring-fen round the edges was immediately apparent. Between the birch wood and drier heath round the edge of the area and the *Cladium* and *Phragmites* on deep peat in the centre was a rich and varied vegetation ranging from patches of *Sphagnum* to areas dominated by *Schoenus* where there was evidently an abundance of highly calcareous water. Several members spent some time looking for and finding interesting bryophytes, sedges and orchids. One or two other smaller but similar fens near by were more briefly visited and finally the larger Market Weston Fen was inspected where there were obvious signs of grazing. Here again orchids were photographed and collections of freshwater fauna made from the dyke and ditches.

On Sunday a choice of excursions was provided. A group of members led by Mr Bingley visited habitats on the Stour estuary. First the saltmarsh at Wrabness Point was examined where the Puccinellietum is being invaded by *Spartina townsendii*, which was introduced at Cattawade in 1923. Then the sweet-chestnut coppice at Stour Wood was visited where there is a rich herb layer on London clay with gravel patches. The party then drove to Kirby-le-Soken, walked along the ¾ mile causeway to Horsey Island, examined the saltmarsh and compared it with that at Wrabness. After tea at Frinton the party returned to Flatford Mill. The second group were taken by Mrs Bingley on a tour that was architectural and historical rather than strictly ecological but none the less very interesting and enjoyable. Among the Suffolk villages and churches visited were: Stoke by Nayland, Nayland, Wiston, Sudbury, Clare, Long Melford, Lavenham, Kersey and Hadleigh. On the evening of Sunday Mr Bingley gave an illustrated talk on Shingle Street and its vegetation.

The next day the meeting journeyed by bus through Ipswich to Staverton Thicks. Here we were met by Dr Rose who proceeded to demonstrate this remarkable wood. Dominated by oaks and what must be some of the largest hollies in the country, the ground flora is largely *Pteridium*, but epiphytic bryophytes were numerous. We then drove on to Shingle Street, where in fine weather we spent several enjoyable hours. The shingle bank itself attracted first attention; *Lathyrus japonicus* was prominent as an initial colonizer, followed by *Arrhenatherum elatius* and *Rumex crispus* and then by a fairly continuous turf of *Festuca rubra* and a number of maritime and other plants. There were also lines where drift had accumulated and *Beta maritima* grew. Some time was spent examining the series of lagoons and their surrounding vegetation. *Ruppia*, *Zannichellia* and various algae grew in the lagoons; *Halimione*, *Suaeda maritima* and

Salicornia were prominent above the margins. Time did not allow a detailed examination of the relict sand-dune area or the saltings to the north-west. After returning to the Mill, the Society foregathered again at Dedham for an enjoyable informal dinner.

On the final day of the meeting the remaining members paid a visit to the Ministry of Agriculture, Fisheries and Food's Fisheries Laboratory at Burnham on Crouch. Firstly we were taken on the laboratory's research vessel down the Crouch and then up the River Roach to some of the commercial and experimental oyster grounds. Here we were shown dredgings of oysters and other animals of the estuary bottom. On return to the laboratory we toured the various rooms and were shown the research in progress. Finally we were taken to Dr Butcher's home where Mrs Butcher provided an excellent tea. We are most grateful to Mr Simpson and all the other members of his staff and to Mrs Butcher for a most interesting and enjoyable visit.

Although the small numbers attending the meeting meant that the proceedings were pleasantly informal, uncrowded and unharried, they did poor justice to the hospitality the Society received at Flatford Mill, or to the wealth of ecological interest provided. We are very much indebted to Mr Bingley and all his staff for the considerable trouble they took to ensure that we were shown places of real interest, provided with full explanatory details and given every attention and comfort; a most interesting, enjoyable and instructive meeting.

E. D. Le Cren

THE BRITISH ECOLOGICAL SOCIETY

Officers and Council for the Year 1960

President: J. B. CRAGG — *Vice Presidents*: D. CHITTY, P. W. RICHARDS

Honorary Treasurers:

F. H. WHITEHEAD — Imperial College Field Station, Selwood Park, Sunninghill, Berks.

J. L. HARPER (receives subscriptions) — Department of Agriculture, Parks Road, Oxford.

Honorary Secretaries:

C. H. GIMINGHAM (membership) — Department of Botany, University of Aberdeen, Old Aberdeen.

E. D. LE CREN (Council) — The Ferry House, Far Sawrey, Ambleside, Westmorland.

Honorary Editors of the Journal of Ecology: P. W. RICHARDS and D. E. COOMBE

Honorary Editor of the Journal of Animal Ecology: H. C. GILSON

Council (together with Officers as above):

Retiring: 1961	1962	1963	1964
D. J. CRISP	M. ASHBY	F. FRASER DARLING	A. R. CLAPHAM
M. W. HOLDGATE	F. J. BINGLEY	J. L. HARLEY	W. H. DOWDESWELL
C. D. PIGOTT	P. GREIG-SMITH	K. H. MANN	E. A. G. DUFFEY
H. V. THOMPSON	L. A. HARVEY	J. WARREN-WILSON	P. J. NEWBOLD

Honorary Editors of the Biological Flora:
A. R. CLAPHAM, D. E. COOMBE, C. D. PIGOTT, P. W. RICHARDS

The British Ecological Society was founded in April 1913, when it replaced the British Vegetation Committee (founded in 1904). The object of the Society is to promote and foster the study of Ecology in its widest sense. This it does by publishing the *Journal of Ecology* and the *Journal of Animal Ecology*, and by holding regular meetings when papers are read and symposia and discussions on subjects of current ecological interest are held. At present these meetings are held in early January, March or April, and July, in London, Oxford or Cambridge or a provincial centre; the July meeting is devoted primarily to excursions to places of ecological interest.

MEMBERSHIP of the Society is open to all, whether or not they reside in the British Isles, who are genuinely and personally interested in Ecology and wish to receive the Society's journals for their own use. The minimum subscription for membership is 40*s*., due on January 1st each year. This entitles members to receive *one* of the two journals, to attend the meetings and make use of other facilities that the Society may offer, to vote in the election of Council and Officers and be eligible for election to Council and Office. For a subscription of 70*s*. members may receive *both* journals.

ASSOCIATE MEMBERSHIP of the Society is open to those who wish only to attend meetings. Associates pay an annual subscription of 7*s*. 6*d*. and do not have the right to receive a journal or vote at a meeting of the Society.

Local Natural History Societies, Field Clubs and other similar bodies are eligible for a special membership of the Society.

Full details of membership and an application form may be obtained on request from either of the Honorary Secretaries.

VOL. 29, NO. 1 MAY 1960

THE JOURNAL OF ANIMAL ECOLOGY

WORLD-LIST ABBREVIATION: *J. Anim. Ecol.*

CONTENTS

PAGE

Alan Burges. Time and size as factors in ecology 1

F. L. Vanderplank. The bionomics and ecology of the red tree ant, *Oecophylla* sp., and its relationship to the coconut bug, *Pseudotheraptus wayi* Brown (Coreidae) 15

J. Phillipson. A contribution to the feeding biology of *Mitopus morio* (F) (Phalangida) 35

L. R. Taylor. The distribution of insects at low levels in the air . . . 45

M. J. Holden and J. Green. The hydrology and plankton of the River Sokoto 65

John MacLeod and Joseph Donnelly. Natural features and blowfly movement 85

D. J. Crisp. Factors influencing growth-rate in *Balanus balanoides* . . 95

R. B. Clark and E. C. Haderlie. The distribution of *Nephtys cirrosa* and *N. hombergi* on the south-western coasts of England and Wales . . . 117

J. P. Dempster. A quantitative study of the predators on the eggs and larvae of the broom beetle, *Phytodecta olivacea* Forster, using the precipitin test 149

H. Barnes and E. S. Reese. The behaviour of the stalked intertidal barnacle, *Pollicipes polymerus* J. B. Sowerby, with special reference to its ecology and distribution 169

C. B. Williams and M. F. H. Osman. A new approach to the problem of the optimum temperature for insect activity 187

Reviews 191

Books received 195

Abstracts 196

British Ecological Society

Spring Meeting, 1958 213

Summer Meeting, 1958 215

Notice to Contributors . . . . . Cover ii

PRINTED IN GREAT BRITAIN IN THE CITY OF OXFORD AT THE ALDEN PRESS
AND BOUND BY THE KEMP HALL BINDERY, OXFORD